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AUSTRALIAN JOURNAL OF ZOOLOGY

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VOLUME 3
NUMBER 2
JUNE 1955

REGISTERED IN AUSTRALIA FOR TRANSMISSION BY POST AS A PERIODICAL

AUSTRALIAN JOURNAL OF ZOOLOGY

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of results of original scientific research in zoology with special emphasis on the descriptive phases

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MELBOURNE

STUDIES ON THE PARASITIC STAGES OF THE CATTLE TICK, *BOOPHILUS MICROPLUS* (CANESTRINI) (ACARINA: IXODIDAE)

By THE LATE L. F. HITCHCOCK*

(*Manuscript received November* 5, 1954)

Summary

Studies were made on infestations of *Boophilus microplus* (Canestrini) established by single applications of large cultures of larvae to cattle. The minimum duration of the larval stage was 4.5 days, and the maximum 13.1 days. Fifty per cent. of the larvae had undergone ecdysis by 5.5 days after attachment. Nymphs commenced to moult 11.9 days after the attachment of the larvae to the cattle, and the last moulted 20.3 days after the infestation of the cattle. Fifty per cent. of nymphs had completed the moult 13.9 days after attachment of the larvae. Male nymphs moulted, on the average, somewhat earlier than female nymphs. Adult males were still present up to 70 days after attachment of the larvae to the cattle. Engorged female ticks commenced to fall 18.9 days after the attachment of the larvae. Fifty per cent. had fallen by 21.9 days, and the last fell at 35.5 days. Climate has little effect on the duration of the stages on cattle.

A diurnal rhythm in the fall of engorged ticks was demonstrated, most ticks falling between the hours of 6.00 and 10.00 a.m.

There is a considerable natural mortality of all stages of the tick on cattle.

The importance of the life history studies to toxicological work is discussed.

I. INTRODUCTION

The cattle tick, *Boophilus microplus* (Canestrini 1887), is the most important ectoparasite of cattle in Australia, transmitting as it does the sporozoan blood parasites responsible for "tick fever", and apart from this, causing losses through reduced production and the expense of control measures.

For more than 50 years almost the only method of cattle tick control practised in Australia has been the treatment of cattle with acaricides, and this is still the most practical approach to the problem. Until the inauguration of C.S.I.R.O. investigations into the cattle tick problem in 1941, arsenical preparations had been used almost exclusively, and in view of the appearance in some places of arsenic-resistant ticks and the general lack at that time of alternative acaricides, attention was early directed to improving the efficiency of arsenical preparations. Existing information on the life history of the cattle tick (Legg 1930) proved inadequate for critical toxicological work and the detailed studies reported in the present paper were undertaken. In investigating the effect and timing of application of chlorinated hydrocarbon and other subsequently developed acaricides, detailed knowledge of the life history of the tick has also been of considerable value.

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II. METHODS

Supplies of tick larvae for establishing experimental infestations were obtained from cultures maintained at Yeerongpilly. The engorged females from which the tick larvae were derived had fallen naturally from artificially infested cattle maintained in stalls. The ticks were gathered from the concrete floor soon after falling, and maintained during the preoviposition and oviposition periods at 30°C and high humidity. The eggs were separated from the spent and dead ticks and placed in incubators at 30°C and relative humidity over 80 per cent. After hatching, the larvae were maintained under the same conditions in mass cultures in glass tubes plugged with cotton wool.

Tick-free cattle from uninfested pastures were placed in concrete-floored stalls, and tick larvae applied to them. If the experiment required infestations to be carried out during the hours of darkness, seed tick cultures were activated by artificial illumination for half an hour before they were placed on the cattle. The floors were thoroughly hosed during the few hours after the application of the seed ticks to wash away any that may have fallen, and thus ensure a definite starting point for each artificial generation. The stalls were isolated by an oil-covered moat from invasion by tick larvae from outside, and the cattle were maintained in them until observations were completed.

Large samples for study were taken by scraping all the ticks from a chosen area with a blunt instrument.

III. RESULTS

(a) *Stages in the Life Cycle of the Cattle Tick*

Detailed anatomical descriptions of the clearly defined parasitic stages of *B. microplus* are given by Fielding (1926) and Cooley (1946). However, it has been found advantageous to recognize certain rather arbitrarily defined stages in the engorgement of the three instars, which are also dealt with in the following notes.

(i) *Larval Stages.*—The larvae lose the power of movement of the legs soon after the abdomen begins to enlarge.

(1) *Undistended Larva.*—This parasitic stage is similar to the six-legged, free-living larval tick or "seed tick", except that the mouthparts are embedded in the tissues of the bovine.

(2) *Medium-sized Larva.*—Engorgement has proceeded to a point at which the abdomen of the larva has elongated slightly, and become pointed posteriorly. The colour of the abdomen is dark grey. The power of movement of the legs is retained.

(3) *Semi-engorged Larva.*—At this stage the larva is approximately full-sized, but it is creamy in colour with grey blotches dorsally and can be indented somewhat by pressure. The legs are rigid.

(4) *Engorged Larva.*—The integument is shiny and tightly distended, and creamy or white in appearance. The legs are rigid.

(ii) *Nymphal Stages.*—In the nymphal stage too the power of movement of the legs is lost soon after the abdomen begins to enlarge.

(1) *Undistended Nymph.*—This flat-bodied, eight-legged stage is disclosed by the moulting of the engorged larva. There are clearly marked grooves on the dorsal surface. It is light brown in colour immediately after moulting, but changes to a slaty grey before the body proportions alter as engorgement progresses. The unfed nymph is able to crawl if detached from the host. It is not known to what extent movement normally takes place from the site of attachment of the engorged larva.

(2) *Medium-sized Nymph.*—This stage corresponds to that of the medium-sized larva but it cannot move its legs. The dark grey body is flat and narrow, with well-marked dorsal grooves. There is limited abdominal distension.

(3) *Semi-engorged Nymph.*—This stage has the general dimensions of the fully engorged nymph, having broadened considerably more than the previous stage, but it has longitudinal corrugations dorsally and is generally greyish, the dorsal pattern not being as sharply defined as that of the fully engorged nymph. The body is not fully distended, but can be indented by pressure. The legs are rigid.

(4) *Engorged Nymph.*—In this stage the tick cannot crawl. It is brown in colour, with a dark dorsal pattern, and the malpighian tubules are clearly visible through the dorsal integument. The cuticle is tightly distended, and no grooves are visible.

(iii) *Adult Stages.*—All adult stages retain the power of locomotion.

(1) *Male Adult.*—The male adult has relatively longer legs than the nymph. It is able to withdraw its mouthparts at will and move around on the body of the host. No engorgement occurs. The colour of the body is dark brown.

(2) *Undistended Female Adult.*—This stage has a small, flattened body and eight legs somewhat longer than those of the male. It is light to dark brown in colour.

(3) *Medium-sized Female Adult.*—This stage exhibits moderate dorso-ventral thickening, but the lateral dimensions are little bigger than those of the preceding stage.

(4) *Semi-engorged Female Adult.*—These females have attained about half their fully engorged size. Usually at this stage the female is brown in colour, rather flattened, and grooved dorsally.

(5) *Engorged Female Adult.*—These are fully replete females, about to drop from the host. At this stage the colour is usually grey-green.

(*b*) *Duration of the Parasitic Life History Stages*

This study was carried out with five bovines which had never previously been tick-infested, nor treated with any toxic material. The animals were infested serially at intervals of 0.2 day, so that at the end of 24 hr hosts were available bearing ticks ranging in "parasitic" age from 0.2 to 1 day.

The seed ticks spread all over the body of the animal soon after they had been placed on it. General observations suggested that over 95 per cent. of them settled and embedded their mouthparts within an hour. There is evidence that a very small proportion may have wandered in the hair of the beast for as long as 3 days.

TABLE 1

THE PARASITIC LIFE CYCLE OF B. MICROPLUS ON ARTIFICIALLY INFESTED CATTLE

Stage	Period after Infestation at which Stage Observed (days)		
	First Observed	Attained by 50% of Population	Last Observed
Undistended larva	—	—	3.5
Medium-sized larva	—	—	5.5
Semi-engorged larva	—	3.2	7.7
Engorged larva	3.3	3.7	8.7
Undistended nymph	4.5	5.5	13.1
Medium-sized nymph	8.1	9.2	18.9*
Semi-engorged nymph	8.7	10.7	18.5*
Engorged nymph	9.7	11.8	20.3
Male adult	11.9†	—	—
Undistended female adult	12.9	13.9	21.0
Medium-sized female adult	16.5	18.9	—
Semi-engorged female adult	17.7	21.0	—
Engorged female adult	18.9	21.9	35.5

* Samples from different animals.

† Latest record of moulting from nymph, 19.7 days.

The first samples were taken 72 hr after the first beast was infested. Then and thereafter at 24-hr intervals, substantial scrapings were taken from each beast, until 21 days after the first beast had been infested, when it was impracticable to continue the sampling. No area was scraped twice. No sample contained less than 200 ticks and most contained very many more.

The samples were sorted in the laboratory into the various classes enumerated above and the percentage of each stage in each sample calculated. The minimum age at which each stage was attained, the latest record of each stage after the time of infestation, and the time at which 50 per cent. of the population had completed each stage are presented in Table 1.

The cumulative percentages of the ticks completing each life history stage were plotted on probability paper, and curves hand-fitted to these individual points were converted to curves showing the straight cumulative percentage of the population completing each stage (Fig. 1).

The curve indicating change from engorged nymphs to young adults is somewhat steeper than the lines for change to engorged and semi-engorged nymphs preceding it. Probably this is evidence of a subjective element in the assessment of the proportion of the earlier stages mentioned, there being a tendency to classify ticks as in the next higher stage more readily when they first appear than when they become numerous. Apart from this the curves for the stages earlier than the engorged nymph call for little comment.

Engorged nymphs can be sorted into two fairly clear-cut size groups, the smaller nymphs being destined to give rise to males. However, there is a certain overlap, and the presentation of separate curves for the sexes in the nymphal stage has not been attempted.

The curves for the adult female stages, so far as they can be constructed, are presented in Figure 1; but as the females comprise only a fraction of the samples (the balance being immature stages and males), and all curves up to and including the moulting of engorged nymphs were based on the entire samples, it will be appreciated that they are differently based.

Males tended to moult earlier than females (Table 1). When the engorged females fell, the males remained on the host. In this experiment the study of the males was not carried beyond the 21st day after infestation of the cattle, but in an earlier experiment it was found that appreciable numbers of males were still present on a beast 43 days after infestation (15 days after the disappearance of the last female in this experiment) and a few persisted until 70 days after infestation of the cattle.

A point of interest about the early stages of the nymph and adult female is the comparatively long period spent after moulting before any substantial enlargement of the body occurs. Lees (1952) found that, during a similar period in the adult stage of *Ixodes ricinus* L., the integument of the female was undergoing relatively enormous thickening, presumably an adaptation to the need for accommodating the huge blood meal which is subsequently ingested.

Engorged females commenced to fall on the 18th day, thus interfering with the presentation of the other life history stages as percentages of the total population. The progressive fall of engorged females, expressed as a percentage of the ultimate total, is illustrated in Figure 2. This is based on two only of the five animals originally infested, as the remainder were too lightly infested by the time females commenced to fall to be worth study. Data from another artificially infested animal (animal 1) are also included in the figure. The prolongation of the terminal portion of the curve in Figure 2 results from the tendency repeatedly observed in artificial

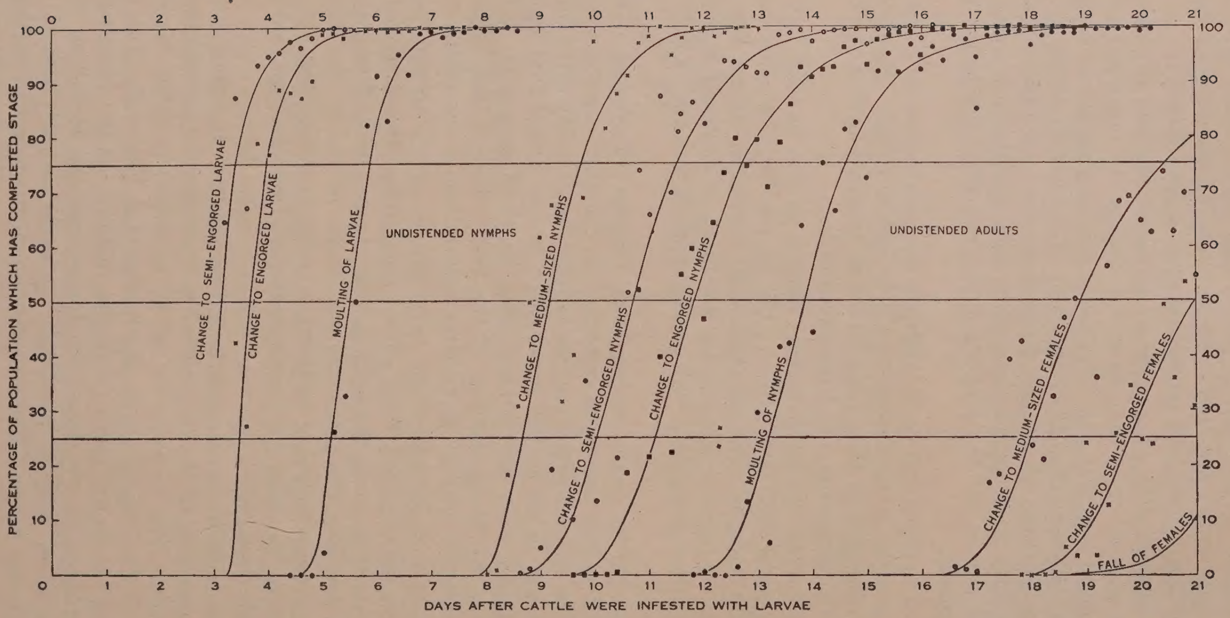

Fig. 1.—Cumulative percentages of population of *B. microplus* completing life history stages in artificial infestations on cattle.

infestations of *B. microplus* on cattle for a few individuals to take considerably longer than the rest of the population to reach a specified stage of development. This tendency is manifested to a somewhat lesser extent in the larvae and nymphs than in the adult females (Fig. 1). A factor possibly contributing to this feature of the curves is the failure of some larvae to settle until a few days after application to the cattle.

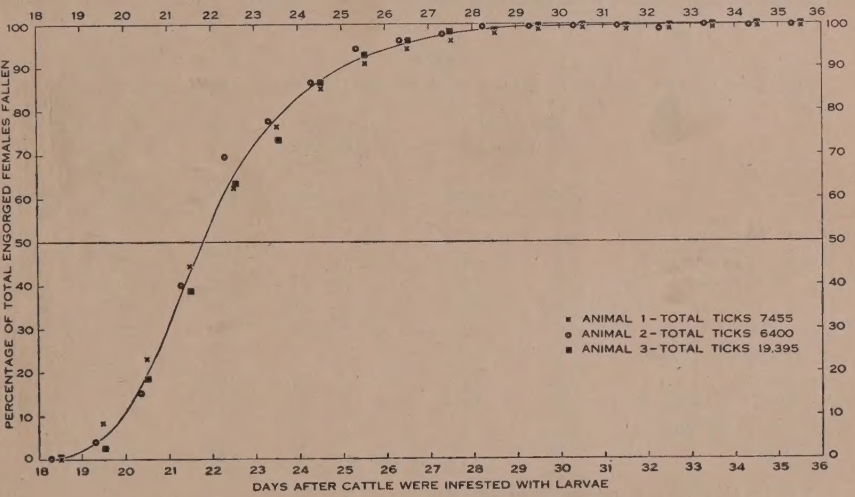

Fig. 2.—Cumulative percentage fall of engorged females of *B. microplus* in artificial infestations on cattle.

(c) *Effect of Seasonal Temperature Variation on the Duration of the Parasitic Life Cycle of* B. microplus

Table 2 summarizes the values published by various authors for the duration of the instars of *B. microplus* in different parts of its geographic range.

Legg (1930) found that there was little difference between the winter and summer duration of the parasitic life cycle at Townsville, north Queensland (Table 2). Observations by the present writer at Yeerongpilly, southern Queensland, where the winter is a good deal colder than at Townsville, confirm this. Ticks from six animals infested during the winter months showed modal fall early on the 23rd day, while a corresponding test in summer resulted in modal fall late on the 22nd day. The observations of Sapre (1940) were carried out in India at an altitude of 7500 ft, where the author stated that temperatures permitted the development of only two generations a year. It is evident from the data in Table 2, and those cited above, that the temperature of the environment of the bovine host has little effect on the duration of the parasitic life cycle of *B. microplus*.

(*d*) *Diurnal Rhythm of Fall of Engorged Females*

It is often stated by cattlemen that engorged ticks are most numerous on the cattle in the early morning, but drop off in considerable numbers in the first few hours of daylight. Indications that this might be so were obtained by Mr. P. R. Wilkinson (personal communication) during observations at Rockhampton on stalled animals, and an experiment to investigate the point was carried out at Yeerongpilly with six artificially infested animals. On the 20th, 21st, and 22nd days after infestation, falling female ticks were collected and those gathered in each successive 4-hr period were counted separately. There is strong evidence from these data (Table 3) that a peak in the numbers of females falling from each animal occurred daily between 6.00 and 10.00 a.m. The animals were exposed to diurnal variation of temperature, light, and other physical factors. They were also fed each morning at 8.00 a.m., which would probably have involved more disturbance than the regular collection of ticks, so host activity may have been one factor influencing the time of the peak tick fall. If so, the resumption of activity after nocturnal resting of cattle in pasture may produce the increased early morning fall of engorged ticks that is stated to occur. A diurnal rhythm in tick fall would not affect Figure 2, which is based on pooled collections over 24-hr periods.

TABLE 2

DURATION OF THE PARASITIC STAGES OF B. MICROPLUS (DAYS AFTER INFESTATION)

Authority	Moulting of Larvae		Moulting of Nymphs		Falling of Engorged Females		
	First	Last	First	Last	First	Last	Mode
Hooker, Bishopp, and Wood (1912), U.S.A.	6	9	14	19	22	29	22-25
Legg (1930), Australia	6*	10	13	20	20	34	22
	6†	10	13	21	20	35	24
Sapre (1940), India	7	9	14	18	24	29	26
Ault (Lahille) (1948), Argentine	5	9	17	23	23	29	—
Tate (1941), Puerto Rico	9	11	14	19	20	27	22-23
Hitchcock (this paper), Australia	5†	9	13	21	19	36	23

* Data in this row obtained in summer.

† Data in this row obtained in winter.

(*e*) *Mortality of Ticks on Cattle*

In the study of the duration of the parasitic stages of *B. microplus*, dead ticks were frequently found in the samples, death being recognizable in the non-mobile stages by drying or decomposition of the body contents.

To obtain some quantitative data on this subject, large samples of ticks were scraped from a number of areas on each of three naturally infested animals which had received no acaricidal treatment for 12 months. Of 2588 ticks examined from one animal, 17.8 per cent. were dead, 233 ticks

TABLE 3

DIURNAL RHYTHM OF THE FALL OF ENGORGED FEMALES OF B. MICROPLUS FROM STALLED CATTLE

End of Collection Interval	Percentage of Total Ticks Collected: Animal No.					
	1	2	3	4	5	6
2 p.m.	3.7	1.7	2.9	3.5	3.0	2.4
6 p.m.	6.4	2.6	2.5	5.6	3.6	10.0
10 p.m.	4.1	5.7	1.1	4.3	0.7	2.3
2 a.m.	2.8	24.1	6.6	5.3	10.3	1.2
6 a.m.	9.6	5.0	4.0	5.3	3.6	2.9
10 a.m.	16.2	11.5	14.3	33.0	15.5	11.0
2 p.m.	2.0	0.3	4.3	5.3	5.5	7.2
6 p.m.	6.0	2.1	4.0	5.3	6.1	10.2
10 p.m.	2.0	2.4	1.5	5.6	1.4	2.4
2 a.m.	2.5	7.1	1.2	4.0	3.1	3.1
6 a.m.	5.0	2.6	10.7	2.3	4.2	1.2
10 a.m.	14.5	11.3	11.1	6.0	13.7	14.4
2 p.m.	2.1	1.4	7.0	1.5	7.9	2.4
6 p.m.	5.4	2.8	10.0	3.6	4.6	6.9
10 p.m.	1.9	2.3	4.6	3.1	2.1	3.1
2 a.m.	1.5	7.8	4.8	2.9	5.7	1.7
6 a.m.	3.2	1.6	4.1	0.9	1.6	1.4
10 a.m.	10.1	7.9	4.7	1.5	6.4	13.1
2 p.m.	1.0	0.5	1.3	1.0	3.0	3.9
Total ticks collected	2406	10,874	13,334	1547	8208	3346

TABLE 4

NATURAL MORTALITY OF VARIOUS STAGES IN SAMPLES OF B. MICROPLUS FROM UNTREATED, NATURALLY INFESTED CATTLE

Stage	Number Examined	Percentage Dead
Unengorged larvae	53	3
Engorged larvae	32	6
Unengorged nymphs	168	21
Engorged nymphs	564	15
Male adults	1354	14
Undistended female adults	173	36
Medium-sized females	89	43
Semi-engorged females	133	27
Engorged females	22	26

from the second animal included 24.9 per cent. of dead, and 200 ticks from the third animal included 17.8 per cent. of dead. The ticks from the first animal were sorted, and separate mortality counts made on each stage (Table 4). It is apparent that there is quite a considerable mortality of ticks on the host; but as dead ticks are not shed immediately, there is some accumulation of them on the skin.

The exact effect of mortality on the curves of the various life history stages cannot be assessed without further data. If mortality were shown to be density-dependent it would, of course, be an important factor.

IV. Discussion

Although the data in the present paper are more complete than any hitherto published, the variation between successive samples is nevertheless considerable, and as yet no adequate reason can be advanced for this. There is no evidence of difference between the animals in the rate of development of the ticks on them. Snowball and Norris (personal communication) observed that ticks under the folds of the flanks of bovines passed through the early stages at least of the life history somewhat more rapidly than on the general body surface, but the effect is insufficient to account for the variability in the samples, even if anomalies were found to occur in regions other than the flank. Sampling error is probably responsible for most of the variation.

The data presented in the present paper have greatly facilitated toxicological studies on parasitic ticks. For example, in assessing survival after spraying or dipping experiments, results are obscured for some time by the presence of adhering dead ticks, and it is necessary to await the natural shedding of these. By the time this has occurred the survivors may be considerably older than at the time of treatment, but the data presented in this paper permit the determination of their probable age at the time of treatment. The most valuable use for the data lies in determining the "protective period" of toxicants. Some acaricides, of which DDT is the outstanding example, have an important residual toxicity, which prevents larvae from establishing themselves on the cattle for some time after dipping. Various formulations have potentially greater persistency than others, and by studying the rate of reinfestation of the cattle the respective protective periods can be ascertained. The mere detection of seed ticks attached to cattle is not a sufficient indication that toxic residues are no longer present. Experience has shown that the first seed ticks attaching after cattle are dipped in DDT usually die, but frequently it is difficult to decide without good illumination and magnification whether they are alive. The protective period is therefore best determined from the study of a firmly re-established infestation, of which the stages are more readily visible to the naked eye. Back calculation from the time of appearance of advanced or engorged nymphs, or preferably, newly emerged and surviving adults gives the most reliable evidence on protective periods. In practice it is not always possible to time examinations so that these life history stages are available, and earlier stages have to be used. Where possible it is preferable to avoid the use of arbitrarily defined stages such as medium-sized and semi-engorged nymphs.

Hitchcock and Mackerras (1947) used the minimum known age of stages in determining protective periods. Norris, Roulston, and Snowball (1950) pointed out that the mean was preferable to the minimum, because of the much higher probability that any individual tick would have had a life cycle of this length rather than the minimum. The use of the minimum instead of the mean introduces an error which becomes relatively greater as protective periods become shorter.

V. ACKNOWLEDGMENTS

The author is indebted to Mr. W. R. Horne for technical assistance in carrying out the life history studies. Mr. R. A. J. Meyers assisted in the work on the diurnal rhythm of fall of engorged ticks. Thanks are due to Mr. G. A. McIntyre for the construction of the curves in Figure 1.

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STUDIES ON MARSUPIAL REPRODUCTION

IV. DELAYED BIRTH IN PROTEMNODON EUGENII DESMAREST

By G. B. Sharman*

(*Manuscript received November* 11, 1954)

Summary

Previous reports of hypertrophied anterior vaginal canals, which serve as ducts for the reception of spermatozoa, in macropod marsupials, are briefly discussed. These have been considered by earlier workers as spermathecae in which spermatozoa are stored for long periods.

In the macropod marsupial *Setonix brachyurus* Quoy & Gaimard it has been shown that spermatozoa are not stored by the female. Delayed birth in this species is due to the storage (in the uterus of lactating females with young in the pouch) of a quiescent unimplanted blastocyst. A brief redescription of earlier work on *Setonix* is included.

A study has been made of the macropod marsupial *Protemnodon eugenii* Desmarest, in which the anterior vaginal canals become greatly hypertrophied at oestrus and which, following copulation, become filled with seminal fluid. In spite of the large numbers of spermatozoa present only one egg — that of the current ovulation — is fertilized. There is no evidence of storage of spermatozoa. The occurrence of quiescent unimplanted blastocysts in the uteri of females suckling young in the pouch shows that delayed birth in *P. eugenii* is strictly comparable with the case of *S. brachyurus*, and is not due to storage of viable spermatozoa by the female.

I. INTRODUCTION

During pro-oestrus and oestrus certain macropod marsupials exhibit greatly hypertrophied anterior vaginal canals which, following copulation, serve as ducts for the reception of spermatozoa (Stirling 1889; and others). It has become customary to refer to these distended, thin-walled portions of the vaginal complex as receptacula seminis (Jones 1923, 1944; Pearson 1946, 1950). It is the orthodox belief that, in primitive marsupials, parturition was by way of the lateral vaginae; but following the adoption of pseudo-vaginal parturition these no longer serve as birth canals. Pearson and de Bavay (1953) consider that the lateral and anterior vaginal canals are, in recent marsupials, concerned mainly with the storage of spermatozoa and that the efficiency of these spermathecae is improved by the caudal plugs which they have described in polyprotodont marsupials. These authors, citing Jones (1923), think it "not unlikely that in certain of the more specialized marsupials such as the Kangaroos, a single supply of spermatozoa may be retained in the spermathecae for a relatively long period and in such circumstances would be available to fertilize two different sets of ova".

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While investigating reproductive processes in a macropod marsupial (*Setonix brachyurus* Quoy & Gaimard), Sharman (1955*b*) found that parous females sometimes produced young after isolation from males for periods of up to about 5 months. In this species the normal gestation period is 27 days. No evidence of sperm retention was found but it was shown that delayed birth was due to the prolonged storage of a quiescent blastocyst in the uterus of the lactating female. This blastocyst results from fertilization at post-partum ovulation (which occurs shortly after normal gestation and birth) and will proceed to normal development in the event of loss of the foetus from the pouch. It has, however, been shown (Waring *et al.* 1955) that *Setonix*, unlike other macropods, does not exhibit hypertrophy of the anterior vaginal canals at oestrus.

A small colony of the macropod marsupial *Protemnodon eugenii* Desmarest (the tammar) has been established in the yards of the Department of Zoology. Several specimens of this species produced young in the absence of males, after foetuses were accidentally lost from the pouch. Urogenital systems from oestrous females exhibit enormously hypertrophied anterior vaginal canals (Plate 1, Fig. 1) in which sperm may be detected following copulation. A study was therefore made in order to decide whether the spermatozoa persisted in these canals during suckling of the pouch foetus, or whether delayed birth could be due to the storage of an unimplanted blastocyst as in *Setonix*.

II. Material and Methods

A large series of reproductive systems of *Protemnodon eugenii* have been studied and three of these are relevant to the present paper. In the first, that of an oestrous female collected in the wild, the anterior vaginal canals were greatly hypertrophied. The oestrous condition was verified by the presence of a blood spot, marking a newly ruptured follicle, on one ovary. A second urogenital system was obtained from a female in the Department's colony which died 10 weeks after observed copulation. Examination of the pouch at the time of mating revealed the presence of a newly born foetus which was still occupying the pouch when its mother died. The third urogenital system was taken from a lactating female, collected in the wild. This specimen had a large, but hairless, foetus in the pouch.

A small blastocyst was isolated from one uterus of the lactating *Protemnodon* collected in the field, the method used being as previously described (Sharman 1955*b*). The various organs of the reproductive systems were studied in serial section. Sections were cut at 7-12 μ, stained in Heidenhain's haematoxylin, and counterstained with eosin.

III. Results

The reproductive processes of *Setonix brachyurus* (the quokka) have previously been described in detail (Sharman 1955*a*, 1955*b*; Waring *et al.*

1955). In this species the lumen of the anterior vaginal culs-de-sac becomes enlarged during pro-oestrus and, following copulation, becomes filled with seminal fluid. At the time of fertilization spermatozoa are found in the uteri and oviducts and are lodged in the egg membranes (Plate 2, Fig. 1). In contrast to the condition found in the oestrous *P. eugenii,* no enlargement of the anterior vaginal canals occurs (cf. Plate 1, Figs. 1 and 3). No spermatozoa are found more than a week after copulation. In females with pouch young which have copulated at post-partum oestrus a small unimplanted blastocyst occurs in one uterus (Plate 2, Fig. 2). It has been shown (Sharman 1955*b*) that this blastocyst proceeds to normal development following removal of the foetus from the pouch or, in domestic females, following emergence of the pouch foetus.

The reproductive system of the oestrous *P. eugenii* shows a general resemblance to that of the oestrous *Setonix*. The stage studied here is taken from a tammar about 1 day after copulation and the as yet unfertilized egg is in the process of extrusion from a ruptured follicle in one ovary. Spermatozoa are common in both uteri and oviducts. Apart from the larger size of the reproductive system of *P. eugenii* the only remarkable difference between the two species is in the nature of the anterior vaginal canals. In *P. eugenii* (Plate 1, Fig. 1) these are thin-walled, enormously hypertrophied, and filled with seminal fluid containing abundant spermatozoa. As in *Setonix* the anterior vaginal culs-de-sac are enlarged and filled with seminal fluid. Histologically the reproductive systems of the two species are similar. In both, mitoses are common in uterine lumen and glandular epithelia and the degree of cornification of the lateral vaginae of the tammar (Plate 2, Fig. 3) is within the range found in oestrous quokkas.

If the explanation of delayed birth in the tammar is to be sought in terms of storage of spermatozoa it is natural to suppose that these would be found in the reproductive system of the lactating female. However, in such females (Plate 1, Fig. 2) the anterior vaginal canals are of small size and spermatozoa are not found here or elsewhere in the reproductive system. At the time of a previous communication (Sharman 1955*b*) we were unable to entirely exclude the possibility of storage of spermatozoa in marsupials other than the quokka, although we considered that previously reported cases of delayed birth in macropod marsupials could be explained in terms of delayed implantation during suckling of a foetus in the pouch. This hypothesis appears to have been fully justified, since both lactating female tammars studied here were found to have an unimplanted quiescent blastocyst in one or the other uterus. The case of the domestic female is especially significant since copulation at post-partum heat was observed. At death this female was still suckling a foetus in the pouch and serial sectioning of the uterus revealed the presence of a blastocyst (Plate 2, Fig. 4). Unfortunately the reproductive system of this female was not fixed until some time after death and this, together with damage during preparation and sectioning, seems to have adversely affected the uterus and contained blastocyst. In the stained section little beyond the outer membranes of the blastocyst remain. There can, however, be no doubt as to its identity and occurrence. A blastocyst of comparable size was also flushed from the uterus of the lactating female taken in the wild. The occurrence of these blastocyst stages in the uteri of females suckling young in the pouch thus establishes the occurrence of delayed implantation in *P. eugenii.*

IV. Discussion

The anterior vaginal canals of *P. eugenii* become greatly hypertrophied at oestrus, and following copulation a large quantity of seminal fluid containing abundant spermatozoa becomes lodged in them. The following observations, however, confirm that delayed birth in *P. eugenii* is due to storage of quiescent unimplanted embryos, and not to storage of viable spermatozoa, by the female:

(i) Females isolated from males for long periods exhibit delayed birth following loss of young from the pouch.

(ii) Post-partum oestrus and copulation have been observed in domestic animals.

(iii) Blastocysts in the quiescent stage have been isolated from the uteri of a domestic and a wild lactating female.

(iv) There is no evidence that spermatozoa are retained in the reproductive system of the lactating female with a young one in the pouch. The anterior vaginal canals, which serve as ducts for the reception of spermatozoa, apparently return to normal size soon after oestrus and during lactation no sperm can be demonstrated in them.

Prior to the work of Sharman (1954 and later papers) reported cases of delayed birth in marsupials were regarded as due to the storage of viable spermatozoa by the female. Jones (1944) considered the "receptacula seminis" of marsupials equivalent to the bouchon vaginal in bats and, as such, concerned with the storage of viable spermatozoa to be used for fertilization when environmental conditions were favourable for the birth of young. Pearson and de Bavay (1953), no doubt impressed by the large volume of spermatozoa found in many marsupial reproductive systems, consider that a single supply of spermatozoa may serve to fertilize ova of two widely separated ovulations. In previously reported cases where sufficient detail has been given, delayed birth has been associated with the lactation period. Thus Jones (1923) records the case of a pair of red kangaroos where the female gave birth to a foetus many months after the death of the male. The intervening period was, however, occupied by the suckling of a pouch foetus. Bowley (1939) recorded "delayed fertilization" in the phalanger *Dromicia* and here the new foetuses appeared in the pouch following the emergence of an earlier family.

So far delayed implantation—the storage by the lactating female of a quiescent unimplanted blastocyst—has been demonstrated in the marsupials *Setonix brachyurus* and *Protemnodon eugenii.* The demonstration of delayed implantation in *S. brachyurus* depends on critical experimental evidence (Sharman 1955*b*), and this is to a lesser extent true of *P. eugenii.* Until experimental evidence is forthcoming for other species there remain no grounds for believing that viable spermatozoa are stored by the female marsupial. On the contrary the observation that delayed birth follows suckling of pouch foetuses may be regarded as good evidence that previously reported cases are due to delayed implantation.

V. ACKNOWLEDGMENTS

The help of Mr. A. J. Jeapes (animal maintenance) and Miss J. Nathan (technical assistance) is gratefully acknowledged. Protected animals have been taken by permission of Mr. A. J. Fraser, Chief Warden of Fauna in Western Australia. Through the courtesy of Captain Bryce Morris, R.N., the author was able to collect specimens of the tammar on the Recherche Archipelago while the guest of Commander G. Rance, R.N., then of H.M.A.S. *Fremantle.* Commander Rance and the officers and ship's company of H.M.A.S. *Fremantle* have given valuable help by collecting wallabies in normally inaccessible places.

Some of the expenses have been defrayed from Research Grants of the University of Western Australia.

The investigation reported here is part of a programme of research on the biology of marsupials mainly financed (including salaries for Miss J. Nathan and the author) by a grant from the Nuffield Foundation, to whom grateful acknowledgment is made. I am indebted to Professor H. Waring for help and criticism during the investigation.

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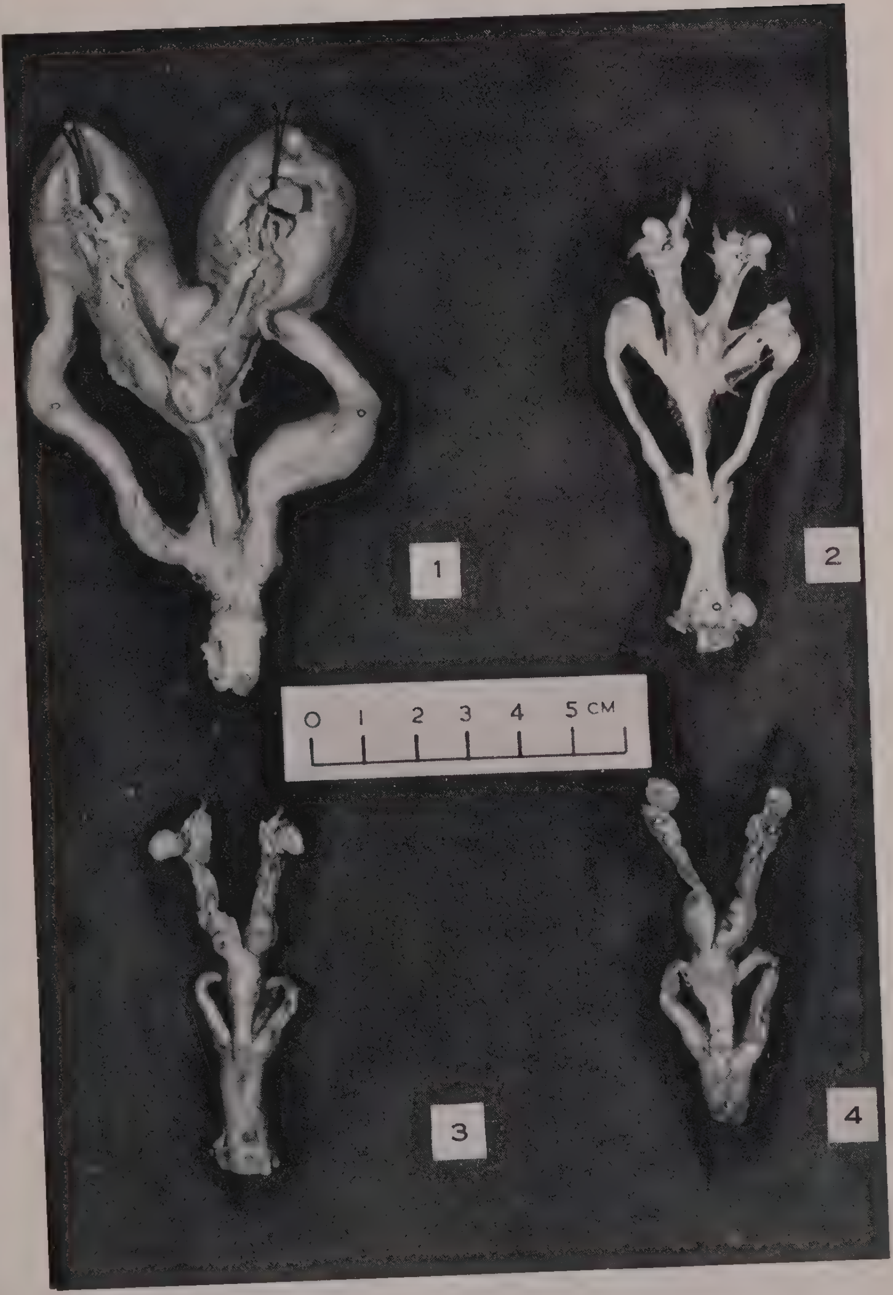
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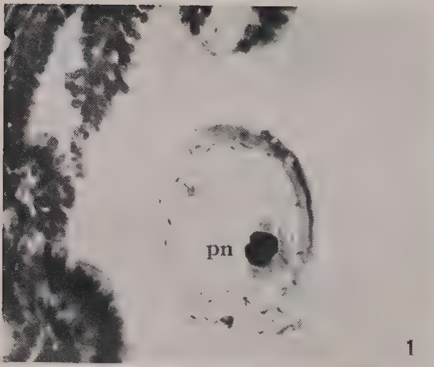
STUDIES ON MARSUPIAL REPRODUCTION. IV



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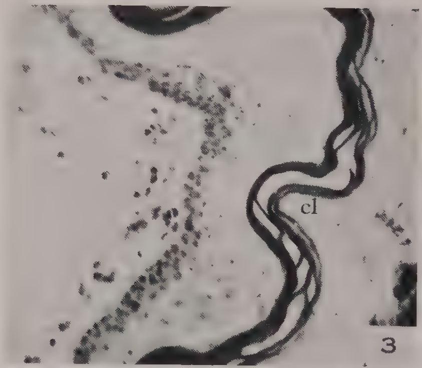

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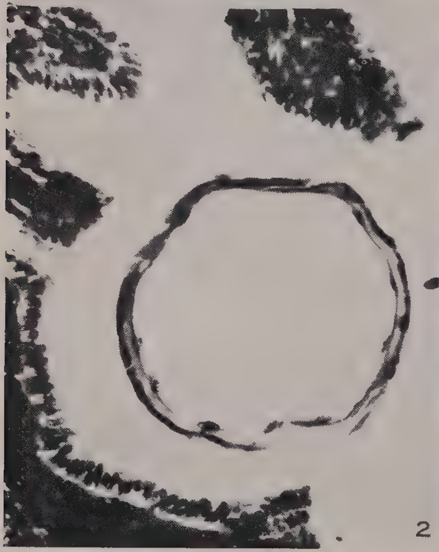

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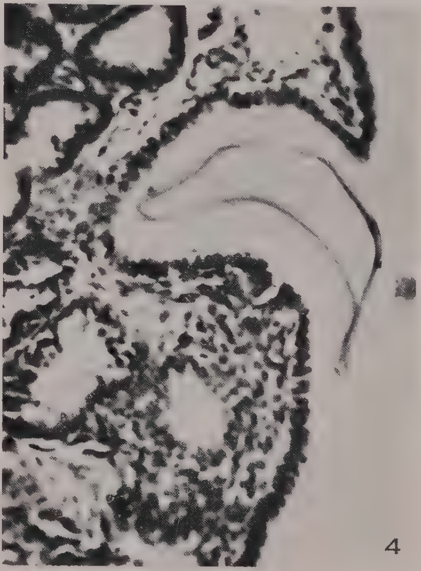

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Fig. 1.—Urogenital system of *Protemnodon eugenii* taken shortly after oestrus. The anterior vaginal canals (above) are greatly hypertrophied and contain seminal fluid.

Fig. 2.—Urogenital system taken from female *P. eugenii* with a 10-week foetus in the pouch. Note the smaller size of the reproductive system and the small diameter of the anterior vaginal canals. The left uterus contains an unimplanted quiescent blastocyst (Plate 2, Fig. 4).

Fig. 3.—Urogenital system from oestrous *Setonix brachyurus*. The median vaginal culs-de-sac are distended and contain seminal fluid. A fertilized tubal egg (Plate 2, Fig. 1) is contained in one oviduct. Compare the anterior vaginal canals with those of *Protemnodon* (Plate 1, Fig. 1).

Fig. 4.—Urogenital system taken from female *S. brachyurus* with a 10-week foetus in the pouch. The system is very similar to that shown in Plate 1, Figure 3, except that anterior vaginal culs-de-sac are not hypertrophied. One uterus contains an unimplanted quiescent blastocyst (Plate 2, Fig. 2).

PLATE 2

All photographs × 150.

Fig. 1.—Tubal egg and small portion of wall of oviduct from the oestrous urogenital system of *Setonix* shown in Plate 1, Figure 3. Two large pronuclei (*pn*) about to fuse and numerous spermatozoa embedded in egg membranes.

Fig. 2.—Unimplanted blastocyst and uterine lumen epithelium from *Setonix* reproductive system shown in Plate 1, Figure 4. Ten weeks have elapsed since fertilization.

Fig. 3.—Cornified lateral vaginal epithelium from oestrous reproductive system of *Protemnodon* shown in Plate 1, Figure 1. Cornified layer (*cl*) at right. Lumen to right of cornified layer.

Fig. 4.—Unimplanted blastocyst and adjacent uterine wall from the urogenital system of *Protemnodon* shown in Plate 1, Fig. 2. Ten weeks have elapsed since fertilization.

OBSERVATIONS ON THE REPRODUCTION AND ECOLOGY OF THE BRUSH-TAILED POSSUM, *TRICHOSURUS VULPECULA* KERR (MARSUPIALIA), IN NEW ZEALAND

By C. H. Tyndale-Biscoe*

(*Manuscript received November* 22, 1954)

Summary

In all 366 adult possums and 139 pouch young were examined. Five samples were collected and a study of a live population was conducted. Data are presented on the relationships of weight, tibial ossification, and sexual maturity, which indicate that two age classes can be distinguished in the fully grown animals on the basis of epiphyseal union of the tibia.

Correlations between body weight, testis length, and the presence of sperm are presented for 53 males.

The reproductive condition of 209 females was examined and successive observations were made on another eight. It is considered that *Trichosurus* is dioestrous and monovular. Pregnancy lasts between 15 and 24 days and is sometimes followed by a post-partum ovulation. Cyclic changes in the uterus and the urogenital sinus are described. The urogenital sinus exhibits marked cornification at oestrus, similar to the vagina of eutherian mammals. Anoestrus in February is followed by increasing reproductive activity in March. By the beginning of May, 90 per cent. of the adult females are pregnant or post-partum and the offspring is carried in the pouch until August or September. Some females may produce a second offspring in October.

Some observations on the movements of individuals are presented.

I. Introduction

The brush-tailed possum,† *Trichosurus vulpecula* Kerr, is probably one of the best-known members of the Australian marsupial fauna. Its widespread distribution in Australia and its successful adaptation to a changing environment have made it a useful species for study. Despite this, however, there is no published account of its reproduction under natural conditions, and observations on its natural history have not been supported by precise field data. In contrast to the many and detailed population studies of eutherian mammals, the field of marsupial ecology has scarcely been explored. The New Zealand situation presents a unique opportunity in this respect, for *Trichosurus,* since its introduction in the last century, has become abundant and widely distributed. It has been deemed a pest because of its depredations in orchards and gardens and the

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† The use of the term possum as the common name for *Trichosurus* is preferred to the term opossum, which rightly refers to species of *Didelphis,* and to the term phalanger which is not commonly used in New Zealand.

damage it causes to indigenous forests, and, consequently, unlimited material can be obtained throughout the year for ecological study.

The present work covers one year's study of the reproduction and ecology of *Trichosurus* and makes no pretence of being an exhaustive treatment. Rather, it is offered as a source of information for future workers in this field.

II. HABITAT

The material was collected on Banks Peninsula, near Christchurch, and in the Haurangi Range, near Wellington, N.Z. Banks Peninsula, which is of volcanic origin, stands out from the Canterbury plains as a well-dissected hilly massif. Before European settlement, it was covered by mixed podocarp forest, but today remnants of this covering are found as isolated stands in the steeper valleys, on the hilltops, and as weathered stumps on the grassland; the peninsula now supports a vigorous sheep farming economy. Rabbits have never become abundant as they have elsewhere in New Zealand, but *Trichosurus* is very numerous and annually several thousand skins of this species are taken from the area. The possums, which are nocturnal, live in the isolated patches of bush and in the farm gardens, and their tracks can be seen traversing wide stretches of open grassland. During the day they sleep in dense thickets, hollow trees, flax clumps, or caves in the basaltic outcrops.

Haurangi Range is in the southern part of the North Island mountain massif and is still covered by indigenous forest. The area carries populations of deer, goats, and pigs, as well as possums. It is divided into blocks which are leased to individual trappers and shooters, and the present sample was collected during private trapping operations.

III. MATERIAL

The material used in this study derives from five sources, some obtained by trapping and some by shooting. The observations taken on the five samples are not fully comparable and the differences in the totals in the subsequent tables are due to this cause.

(*a*) *Haurangi Range Sample*

A total of 664 possums were trapped in the Haurangi Range between April 5 and May 12, 1951, by Mr. L. T. Pracy. On 8 days during this period, the ovaries, urogenital tracts, and pouch young of all females trapped (140) were fixed in Bouin's fluid and preserved in spirit.

(*b*) *Menzies Bay Samples*

Three samples were obtained from this locality on Banks Peninsula in 1953: 55 animals during May 10 to 16, 76 during August 15 to 28, and 23 during November 3 to 7. The first sample was got by trapping, the second and third samples by trapping or by shooting the animals while they were feeding at night.

The following observations were made on these specimens. Weight to the nearest half-pound and the sex were recorded for all the animals. One tibia from each animal was kept. In the males, a smear was made from the contents of the epididymis, and the length of the right testis was measured to the nearest millimetre. In the females, the ovaries were macroscopically examined for corpora lutea. The uteri were dissected and any embryos found were classified according to the 35 stages described by McCrady (1938) for the embryology of *Didelphis virginiana*. The median vagina was dissected and the condition of the median vaginal septum and "pseudo-vaginal" canal (Hill 1900) noted. Late uterine and all pouch young were measured; the head length (H.L.) to the nearest millimetre was taken from the rhinarium to the occipital arch, and the crown-rump length (C.R.L.) also was measured. Pouch young over 12 mm H.L. can be sexed as the scrotum and pouch rudiments are distinct at this age.

(*c*) *Peraki Valley Sample*

A total of 49 possums were taken from Peraki valley, Banks Peninsula, on July 18, 1953, with dogs and rifles. Sex was recorded and one tibia from each animal was kept. This sample gave comparative data on sex ratios, age composition, and sampling methods.

(*d*) *Miscellaneous*

A collection of 43 miscellaneous pouch young in the Zoology Department, Canterbury University College, Christchurch, was drawn upon as supplementary material in connexion with sex ratios of pouch young and the extent of the breeding season. Sex, H.L., C.R.L., and date of capture were recorded for these specimens.

(*e*) *Birdlings Flat Wild Population*

A study of a live population was conducted on a 6-acre area of relict forest at Birdlings Flat, Banks Peninsula (grid reference 060, 250). The forest, consisting of second-tier trees, predominantly *Myoporum* sp. and *Nothopanax* sp., with a fairly open tier of shrubs and herbaceous plants, covers sloping land on both sides of a small creek (Fig. 6). The area is surrounded by unimproved grassland with scattered clumps of gorse (*Ulex europaeus* L.), manuka (*Leptospermum scoparium* Forst.), and flax (*Phormium tenax* Forst.).

Live-trapping was conducted from January 17 to July 11, 1953. Twelve cage traps were set for three consecutive nights every fourth week. Twenty-three animals were marked and there were 20 recaptures. Apple and carrot with aniseed oil were used as bait. Traps were set on promising sites and were not randomly distributed; the most successful places were on sloping tree trunks and at the mouths of caves. On August 30, 1953, in an attempt to collect a large proportion of the marked animals, the study area and a considerable part of the surrounding country were hunted. Twenty-two animals were caught, of which only five were marked.

For observations, the animals were transferred from the cage to a canvas bag and lightly anaesthetized with ether. For individual identification, a system of ear clipping was used. Natural tears, if any, were noted at the time of marking but the special notches were sufficiently distinctive to ensure correct interpretation at recapture. The date and position of capture, sex, and weight to the nearest half-pound were recorded. The reproductive condition of the females was noted, and the H.L., C.R.L., and sex of all pouch young were recorded. Two females were recaptured twice and two were recaptured three times while carrying young in the pouch.

IV. Growth and Age Determination

Measurements of H.L. and C.R.L. were made on all pouch young caught with their mothers during the wild population study at Birdlings Flat. Only four young animals were measured more than once but from these specimens individual rates of growth were calculated. The mean daily rates of increase of H.L. and C.R.L. have been plotted in Figure 1 according to the following equations:

For H.L.,

$$L = 0.383X + 7, \quad \text{or} \quad X = 2.611L - 18.27,$$

and for C.R.L.,

$$L = 1.085X + 15, \quad \text{or} \quad X = 0.922L - 13.82,$$

where L is the length in millimetres and X is the age in days.

The normal form of a growth curve is logistic but for the greater part of active growth, before the upper asymptote is reached, the rate can be considered to be roughly linear, as Southern (1940) assumed for the growth of young wild rabbits. The individual points have been entered on Figure 1 by fitting the initial point for each animal to the mean value. In view of the very limited nature of these data, this growth rate is only approximate and no indication of the expected variation can be assessed. Nevertheless, it does allow the approximate age of pouch young to be calculated and thereby enables the date of birth to be assessed. The oldest of these specimens was still dependent on its mother at the end of August when it was about 4 months old. Broom (1898) and Bolliger and Carrodus (1939) considered that association with the mother lasts 4-5 months, which would mean that a pouch young born in the main breeding season of April-June would leave the parent in September or October. In the small sample collected in November 1953 three young of that year were riding on their mothers' backs but none of the adult females was carrying a large young in the pouch. This suggests that the association of parent and offspring is fairly loose by November, and the young one may be capable of separate existence. A record of the growth of a young male possum was kept by Mr. R. H. Taylor of Lower Hutt, which he kindly made available to me. This animal was on its mother's back on August 20, 1953, when it weighed 13 oz. Association with its mother must have nearly ceased at this date for it lived in a semi-wild state for the next 6 months, and the weight, recorded every fortnight, showed a steady increase to 4 lb on February 16, 1954, after which the animal was not seen again. At this date it was undoubtedly sexually immature, but it is possible that it would have attained sexual maturity by May 1954. Previous authors (Broom 1898; Jones 1924; Wodzicki 1950) have stated that *Trichosurus* is sexually mature at the end of 1 year. In conjunction with the following analysis of the relationship of body weight and tibial ossification to fecundity, Taylor's record appears to support this conclusion.

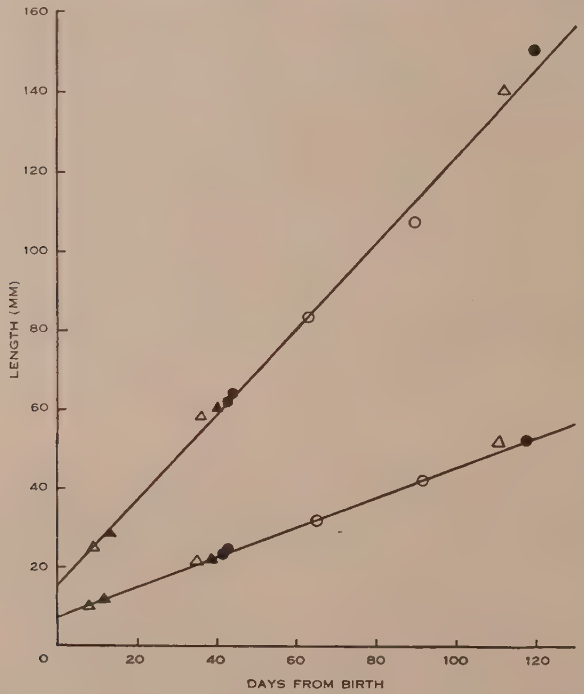

Fig. 1.—The mean growth rates of C.R.L. and H.L. derived from successive observations on four pouch young. The successive points for each animal have been fitted to the line and are represented by individual symbols. △ 5314; ○ 5317; ▲ 53116; ● 53123.

The only account of epiphyseal union in marsupials is Washburn's (1946) description of the sequence in the polyprotodonts *Didelphis*, *Philander*, and *Metachirus*, and in none of these species is union ever complete. In the present study, the occurrence of 63 animals with completely ossified tibiae suggests that *Trichosurus* is similar to most eutherian mammals and unlike the Didelphidae in its epiphyseal development.

In order to use epiphyseal union as a criterion of age in a population study it is necessary to know the mean age at union, and the expected variation from that mean, as shown by Hale (1949) for *Sylvilagus*, and Watson and Tyndale-Biscoe (1953) for *Oryctolagus*. In the present study, the age at which union is complete in the tibia of *Trichosurus* has not been determined, but the samples have been divided into three groups on the basis of tibial ossification. The data so presented will become more meaningful when these groups can be referred to chronological age. The three groups are identified as follows. In group 3 the proximal and distal epiphyses are entirely separated from the diaphysis by cartilage, and the apophysis is separate from the proximal epiphysis; in group 2 the apophysis and epiphysis are united to each other and the proximal and distal diaphysio-epiphyseal sutures appear as clearly defined lines around the two ends of the bone; in group 1 the sutures are entirely ossified.

TABLE 1

THE MEAN LENGTH AND STANDARD DEVIATION OF THE TIBIA IN THREE GROUPS BASED ON TIBIAL OSSIFICATION

Tibial Group:	3	2	1
Number of specimens	33	56	60
Mean length (mm)	92.7	100.7	101.2
Standard deviation	3.3	3.2	3.6

TABLE 2

THE MEAN BODY WEIGHT AND STANDARD DEVIATION IN THREE GROUPS BASED ON TIBIAL OSSIFICATION

Tibial Group:	3	2	1
Number of specimens	44	47	36
Mean weight (lb)	4.5	6.6	7.7
Standard deviation	0.95	1.05	0.86

The relationship of tibial ossification to growth is presented in Tables 1 and 2. In Table 1 the mean lengths of tibiae in each group are given, from which it is apparent that most animals in group 3 have not acquired the full tibial length, whereas the mean lengths of tibiae in groups 1 and 2 are almost equal and represent the adult length for this bone. Similarly, in Table 2 the mean weight of the youngest group, group 3, is significantly less than that of group 2 ($P = 0.005$) but the mean weights of the two oldest groups are not significantly different. The use of tibial ossification as a criterion of age therefore enables the recognition of two age classes among the fully grown animals.

Figure 2 shows that the sexually immature animals, with one exception, are restricted to group 3. Furthermore, those females that are fecund in group 3 and some in group 2 can be shown to be breeding for the first time. If *Trichosurus* attains sexual maturity at the end of the first year it may be assumed that group 3 contains the animals less than 1 year old. Group 3 animals constituted 48 per cent. of the May sample from Menzies Bay and on the present assumption they were the product of the 1952 breeding season. In the August sample this group constituted only 23 per cent., which suggests that some of the animals that were in group 3 in May had grown into group 2 during the intervening 3 months.

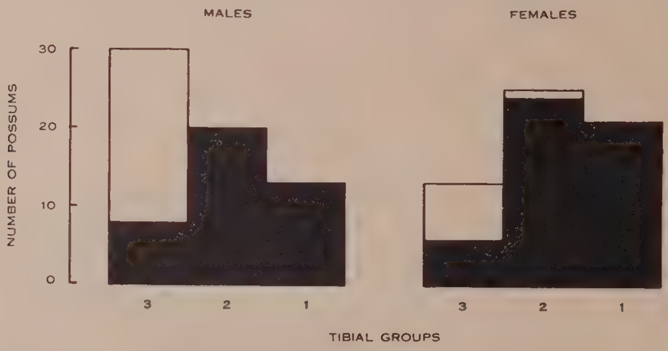

Fig. 2.—The distribution of sexually immature animals (white) in three groups, based on tibial ossification.

The change in the proportions of the three groups from May to August is significant ($P = 0.01$-0.02), but almost certainly sampling bias was a contributory factor in causing this change, for the May sample was trapped and the August sample was trapped and shot. Trapped samples show a high proportion of group 3 animals, whereas shot samples show a low proportion of this group. The significant change in the proportions of the three tibial age groups between the May and August samples from Menzies Bay is too high to be accounted for solely by sampling bias, but it is more likely the result of a real change in the age composition of the population as well as sampling bias. Furthermore, the occurrence of nulliparous group 2 females in the samples supports the suggestion that transition from group 3 to group 2 coincides approximately with the attainment of fecundity. No evidence is at present available to indicate the age at which transition from group 2 to group 1 occurs.

V. The Sex Ratio

The sex ratio in 664 possums, trapped in the Haurangi Range, is 47.5 per cent. males, which is not significantly different from parity ($P = 0.3$-0.5). Similarly, the sex ratio of 222 possums trapped and shot in 1953 is 50.5 per cent. males. If this second sample is broken down according to the method of capture, the several ratios do not differ significantly from parity ($P = 0.3\text{-}0.5$). Nevertheless, sampling bias is suggested, although not apparent statistically, for the sex ratios in the trapped samples are all above 55 per cent. males and in the shot samples are all below 45 per cent. males. However, the Haurangi sample contradicts the supposition that there is a high proportion of males in all trapped samples.

It is unlikely that any sampling bias, acting on the adult sex ratio, can affect the sex ratio of the young in the pouch, and consequently the total records of pouch young have been pooled. Sex could be determined in 128 pouch young, which gave a sex ratio of 54 per cent. males. This ratio is not significantly different from the Haurangi Range ratio but it is interesting that it appears to favour males, in view of the higher proportion of males at birth observed in some eutherian mammals.

VI. Reproduction in the Male

The presence of spermatozoa in the epididymides was used as the criterion of male fertility. Data relating the size and condition of the testes to body weight in 53 possums are presented in the form of a correlation table in Figure 3. Although Figure 3 shows that there is some correlation between testis length and body weight, wide variation even in this small sample is evident. However, correlation between the length of the testis and the presence of sperm is close, whereas there is less correlation between body weight and the presence of sperm. The length of the testes of immature males is distinctly less than in fecund males, and the absence of animals with testes intermediate in length suggests that the growth of the testes immediately prior to the onset of spermatogenesis is

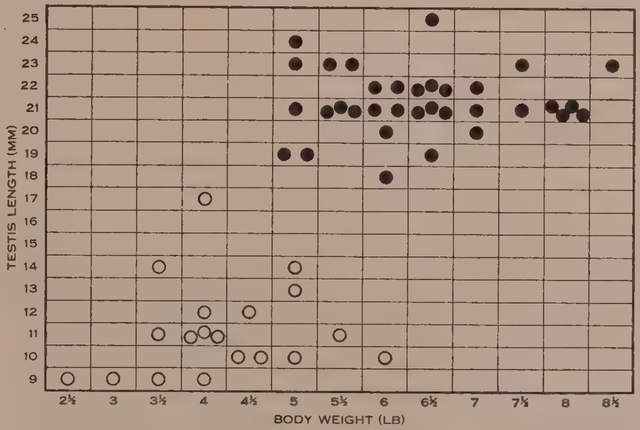

Fig. 3.—The relations between body weight, testis length, and spermatogenesis in 53 males. ○ sperm absent; ● sperm present.

heterogonic. The same pattern of development has been observed in comparable data from several eutherian mammals: the shrew (Brambell 1935), the bank vole (Rowlands 1936), and the wild brown rat (Perry 1945).

From Figure 2 it is seen that all males in tibial groups 1 and 2 and about one-quarter of those in group 3 are fecund. Present evidence suggests that once male possums have attained sexual maturity they do not exhibit any seasonal variation. Males in groups 1 and 2 were examined in May, August, and November, and in all cases they were patently fecund. Bolliger and Carrodus (1938) have observed that a persistent spermatorrhea is characteristic of *Trichosurus* and that individual males show no seasonal variation but void several million spermatozoa in the urine daily.

VII. Reproduction in the Female

(*a*) *Anatomy*

In *T. vulpecula*, the median vaginal septum is present until the first parturition (Hill 1900), when it is ruptured by the passage of the foetus. In the present study it has been assumed that the presence of a complete septum dividing the median vagina indicates a nulliparous condition and no evidence has been found to contradict this assumption.

Hill (1900) noted that in *T. vulpecula* the pseudo-vaginal canal is only patent at parturition. In cross section the passage showed as an uneven tear in the connective tissue between the median vaginal culs-de-sac and the urogenital sinus in a recently post-partum specimen, and had almost disappeared in a female (specimen "C") bearing a pouch young of C.R.L. 18.5 mm. He concluded, from its appearance, that the passage was formed by mechanical rupture during the act of parturition. McCrady (1938) also states that in *Didelphis virginiana* the thin membrane is ruptured as the foetus enters the median vagina.

Table 3 suggests that in *Trichosurus* mechanical rupture is not the sole agency. This table brings together data on the condition of the pseudo-vaginal passage in 93 females, 36 being pregnant. In no case was a foetus found in the median vagina and yet in eight of them nearing term, a blunt seeker passed without apparent hindrance from the median vagina to the urogenital sinus, strongly suggesting that the passage was open. This suggests that hormonal agencies may cause the breakdown of the connective tissue before parturition in an analogous manner to the hypertrophy of the uterus prior to implantation of the blastula. No. 51160 is significant in this context, for it possessed twin embryos in the uterus at McCrady's stage 26 (Plate 1, Fig. 7) and the pseudo-vaginal passage was open. This was the earliest stage of gestation encountered at which the passage was open, and suggests that twin embryos at an early stage of gestation exert the same influence on the passage as a single foetus at a later stage. Wishart and Hammond (1933) reported an analogous phenomenon in the correlation between the prenatal litter size and the duration of pregnancy in the rabbit, large litters having a shorter gestation. Little is known of the hormonal basis of reproduction in marsupials but Bolliger (1946) was unable to cause the pseudo-vaginal passage to develop in *Trichosurus* by administration of oestrogen although he caused excessive distension of the median vagina by this means, to the extent that it ruptured its contents into the coelom. This final effect, as he points out, also suggests that mechanical agencies alone cannot cause the formation of the passage.

TABLE 3

DURATION OF THE PSEUDO-VAGINAL PASSAGE BEFORE AND AFTER PARTURITION IN RELATION TO THE STAGE OF DEVELOPMENT OF THE FOETUS IN 93 PREGNANT OR POST-PARTUM FEMALES

Uterine Stage*	C. R. L. Pouch Foetus (mm)	Passage Patent	Passage Absent
14-26		1†	14
27-29			5
30-32		4	4
33-35	11-13	4	3
33-35	14-16	3	
33-35	17-19	4	1‡
33-35	20-22	2	6
33-35	23-60		43

* McCrady (1938). † No. 51160. ‡ Hill's (1900) specimen "C".

The pseudo-vaginal passage remains open for a variable time after parturition but in all females carrying pouch young over 22 mm in C.R.L. (approx. 7 days after birth) the passage was closed (Table 3).

(*b*) *The Oestrous Cycle and Pregnancy*

(i) *Ovulation.*—From available material it appears that *Trichosurus* is dioestrous and ovulation is spontaneous. In No. 53246, which was nulliparous and had very recently copulated, there was a small regressing corpus luteum on the right ovary and a large new corpus luteum on the left ovary. It is concluded that the regressing corpus luteum was formed at a previous ovulation, which did not result in a pregnancy. Similarly, in No. 511126 there was a small old corpus luteum on the right ovary and a large new one on the left ovary. It was nulliparous and there was a foetus in the left uterus. Here also the old corpus luteum was probably the result of an infertile ovulation. However, in four other females, caught at oestrus, no corpora lutea were observed but one large follicle was found in each, together with several smaller follicles. Sharman (1954) has observed in *Setonix brachyurus* that ovulation follows approximately 1 day after copulation, but in unmated females ovulation occurs independently of copulation. This may also be so in *Trichosurus* and the occurrence of old corpora lutea in nullipari and infertile pari may be due to an initial "silent" heat at the beginning of the season, as Brambell and Rowlands (1936) and others have noticed in eutherian mammals.

Flynn (1930) observed in *Bettongia cuniculus* several pregnant females carrying pouch young and he concluded that *Bettongia* undergoes post-partum ovulation. Sharman (1954) has shown that *Setonix* exhibits the same condition and he showed that the second embryo remains unimplanted until the pouch young is weaned. The present work suggests that in *Trichosurus* post-partum ovulation does occur but is not as invariable as in the two former species. Furthermore, in No. 5328 an advanced uterine embryo was present in the left uterus (stage 32) and a pouch young of C.R.L. 35 mm was found in the pouch, which shows that in this species the product of the post-partum ovulation can become implanted and continue its development. Observations of trappers in New Zealand suggest that two pouch young of different ages rarely survive together in the pouch but no authentic records are available. Several cases have been observed in the present study where a large follicle was present on one ovary of a female pregnant in the contralateral uterus and which would presumably have given rise to a post-partum ovulation. However, post-partum ovulation does not appear to be invariable (as it is in *Setonix*) for in most post-partum females only the corpus luteum of the previous pregnancy and small follicles are found.

With rare exceptions, *Trichosurus* is monovular. That more than one follicle can rupture at a single ovulation is indicated by specimen No. 51160 (Plate 1, Fig. 7) in which twin embryos at the same stage of development were found in the right uterus and two large corpora lutea were found on the right ovary. Twin pouch young have been recorded by Broom (1898) and Wodzicki (1950) but no data were presented by these authors to indicate whether the twins were the result of a single ovulation or were of different ages. The present case is believed to be the first authenticated record of the occurrence of twins in *T. vulpecula.*

The length of gestation in dioestrous mammals does not invite precise determination because of the unknown period between copulation and fertilization. Assuming that the uterine embryo, carried by No. 5328, was the product of a post-partum ovulation following the birth of the pouch young also being carried, a maximum value for the length of gestation in *Trichosurus* can be obtained as the difference between the age of the embryo and the pouch young. By extrapolation from Figure 1 this value is 24 days. This, of course, includes the time intervals between parturition and copulation and between copulation and fertilization. Bolliger and Carrodus (1939) note an instance of a female *Trichosurus* giving birth 16 days after an observed copulation. As the male had been with the female for several days prior to the observed copulation, the length of gestation may be more than 16 days but is unlikely to be much less. The length of gestation in *Trichosurus* is thus between 15 and 24 days and is comparable with the short gestation of other marsupials.

Post-natal association lasts for about 5 months after birth, and during this time the mother is in dioestrus and the ovaries are small; the corpus luteum of pregnancy progressively degenerates during this time and has disappeared, macroscopically, before the young one leaves the pouch.

(ii) *The Uterus.*—The nulliparous females, Nos. 53221 and 53260, are taken to represent the anoestrous condition (Plate 1, Figs. 1 and 3). The body of the uterus is small, and the lumen is small and comparatively smooth; the muscularis is thin and in the mucosa, which is also thin, only scattered glands are present. The epithelia of the lumen and of the glands are composed of high columnar cells, with proportionately large nuclei, which form a distinct layer one cell thick. The epithelium of the lumen is loosely attached to the underlying tissue, and in places is separated from it.

No. 53246, mentioned earlier, had very recently copulated and possessed a new corpus luteum on the left ovary, which indicates that it was in oestrus or immediate postoestrus. Oedema of the uterine mucosa reaches its maximum at this stage so that the uteri appear round and turgid. The median vagina also increases greatly in size and is distended with fluid; 14 c.c. of fluid containing spermatozoa were collected from the median vagina of this specimen. Bolliger (1946) was able to induce this condition in *Trichosurus* by administration of oestrogen. In gross appearance the uterine mucosa was "fluffy", which appearance is apparently due to the accumulation of fluid in the mucosa and to the loosening of the epithelium of the lumen. The glandular tissue has increased and is most compact peripherally (Plate 1, Fig. 2). Towards the lumen the glands are more scattered and this is seen to be due to a diffuse stroma filled with lymphatic spaces. The epithelium of the lumen is free from the underlying tissue over a considerable area and a "secondary epithelium" is beginning to form below it (Plate 1, Fig. 4). The nuclei in the loose epithelium are more closely packed than previously, a feature in which *Trichosurus* resembles *Didelphis* at this stage. Hartman (1923), however, does not mention a loosening of the epithelium at oestrus but this condition has its counterpart in the guinea pig (Stockard and Papanicolaou 1917) and in the white rat (Long and Evans 1922). The cells of the central glands are characterized by large vacuoles at this stage but the peripheral glands have small, basally situated nuclei. This general hypertrophy and loosening of the mucosa in conjunction with secretion of fluid have their counterpart in *Didelphis* and Eutheria. It is commonly interpreted as a preparation for the implantation of the blastula, but it is interesting to note, as Flynn (1930) observed in *B. cuniculus*, that, although *Trichosurus* is monovular, both uteri hypertrophy to the same extent, and it is only later in pregnancy that the gravid uterus can be distinguished macroscopically from the pseudo-pregnant one.

The pregnant condition is described from No. 53219, which was a nulliparous female and contained a 6 mm vesicle in the uterus at McCrady's (1938) stage 21. At this stage the glands of the mucosa appear to be more diffuse than at oestrus and numerous thin-walled blood-vessels are apparent in the stroma. A similar endometrial hyperaemia prior to and during implantation has been reported by several workers reviewed by Amoroso (1952). Histologically the glands are altered. The nuclei, which earlier occupied such a large proportion of the cells, are here confined to their extreme bases (Plate 1, Fig. 8) and the cells themselves are large and thin-walled, indicating that active secretion is taking place. The epithelium of the lumen is similar to the condition at oestrus; it is a semi-detached layer of cuboidal cells and a secondary layer is visible beneath it.

No. 53222 had a new-born young in the pouch still not firmly attached to the nipple and is taken to represent the recently post-partum condition. The uterus at this stage is large, flaccid, and thin-walled. Compared with the pregnant uterus, the mucosa is greatly reduced both in glandular and lymphatic tissue. The glands have returned to a dioestrous condition; the cells are cuboidal and the nuclei are proportionately large. Secretory activity is not apparent, a condition also recorded by Flynn (1930) for *B. cuniculus*. The epithelium of the lumen is closely applied to the stroma and is composed of an indistinct aggregate of cells whose nuclei do not fall into distinct layers (Plate 1, Fig. 5). This layer presumably represents the secondary epithelium referred to above and it raises the question of the fate of the previously overlying, loose epithelium. Flynn (1930) noted a regeneration of the epithelium at parturition in *Bettongia* from the underlying stroma. The cells of the original epithelium underwent degeneration and resorption by leucocytes. Similarly, Hill and O'Donoghue (1914) found that regressive changes take place in the uterine epithelium of *Dasyurus viverrinus* at the end of pseudo-pregnancy. The epithelium does not appear to be shed as a whole but undergoes partial degeneration and desquamation which may so affect the underlying capillaries as to lead to their rupture and a consequent appearance of extravasated blood in the uterine cavity. Amoroso (1952) states that a similar extravasation from maternal capillaries occurs at the end of gestation in *Dasyurus*. Two specimens in the present study had blood in the uterine cavity, together with the remains of foetal membranes. Furthermore, blood appeared on a smear taken from the urogenital sinus of No. 53110 from Birdlings Flat. This female was subsequently recaptured with a pouch young that must have been born very shortly after the smear was taken. In all marsupials so far examined, the foetal membranes are resorbed by the uterus (Amoroso 1952) and the present evidence suggests that in *Trichosurus* both the uterine epithelium and the foetal membranes are resorbed by the uterus at parturition. Numerous leucocytes in the uterus at this stage support this conclusion.

The uterus of the lactating female No. 53259 is in dioestrus and resembles the anoestrous condition described above. However, the glandular tissue of the mucosa in dioestrus is more compact and the muscularis is firmer (Plate 1, Fig. 6). The lumen is slit-like and bounded by an epithelium composed of a single layer of cuboidal cells with large prominent nuclei. The mucosa is well vascularized, erythrocytes are present, but leucocytes are far less numerous than at parturition. The lumina of the glands are small and are surrounded by cuboidal cells with large nuclei.

(iii) *The Urogenital Sinus.*—In structure the urogenital sinus resembles the vagina of Eutheria. The lumen is surrounded by a stratified squamous epithelium about 12 cells deep, which lies on a thick layer of fibrous connective tissue. Surrounding this tissue is a muscular layer of internal longitudinal and external circular muscle fibres. Cyclic changes are only apparent in the epithelium, although the whole organ enlarges at oestrus. During anoestrus and in the immature female, the epithelium presents the appearance of a continuous tissue. The basal cells are cuboidal and these grade into flat, squamous cells near the lumen. In the anoestrous specimen (Plate 1, Figs. 9 and 10) the epithelium shows an incipient stratification into a basal stratum germinativum and a central stratum corneum but all the cells are nucleated.

At oestrus, illustrated by No. 53246 (Plate 1, Figs. 11 and 12), the gross diameter of the sinus has increased and the lumen is larger. Epithelial changes are marked. The stratum corneum, now a distinct layer, consists of small flattened cells with very small, elongated nuclei. Whole blocks of this tissue have sloughed away from the stratum germinativum, which has remained histologically similar to the anoestrous condition. This specimen leaves no doubt that *Trichosurus,* like *Didelphis* (Hartman 1923), exhibits at oestrus an extensive desquamation of the urogenital sinus epithelium similar to the desquamation of the vaginal epithelium of Eutheria.

Desquamation has ceased at most by early pregnancy, for the sinus of No. 53219, which was pregnant, has a clean surface and is composed of an undifferentiated layer of polygonal epithelial cells. The condition at parturition is similar and a few leucocytes can be seen at this stage.

VIII. The Breeding Season

In Australia, *Trichosurus* breeds in the autumn. Bolliger (1940) says that it breeds in March-April around Sydney with a second minor season in August-September, whereas Troughton (1946) gives May-June as the period of birth. The present material suggests that in New Zealand the majority of births occur during March to June, which indicates that there has been no substantial change in the breeding season of *Trichosurus* in its new environment. Data on the breeding season are presented in Tables 4 and 5 and in Figures 4 and 5.

Table 4 shows the distribution of births throughout the year determined from all the available pouch young. The month of birth for each pouch young has been estimated by subtracting the age in days, calculated as a function of H.L. (see Fig. 1), from the date of capture. The samples from the Haurangi Range population of 1951 and the Menzies Bay and Birdlings Flat populations of 1953 are shown separately, but all the other records, which are of animals collected on Banks Peninsula during 1942 to 1952, are pooled together as "Miscellaneous". Only the month and year of capture are known for the latter so the date of birth has been calculated from the 15th day of the month of capture.

TABLE 4

DISTRIBUTION OF BIRTHS IN EACH MONTH ESTIMATED FROM THE AGE OF ALL POUCH YOUNG

Location	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Total
Haurangi Range 1951	7	37	1										45
Menzies Bay 1953		18	17	6				1					42
Birdlings Flat 1953		3	4	1				1*					9
Miscellaneous	7	17	6	2	3	3	1	2		1	1		43

* 1952.

Figure 4 describes the reproductive history of 10 adult females, observed at Birdlings Flat between January and August 1953. The individual histories are reconstructed from the observed condition at the successive dates of capture. The anoestrous condition is shown in white and the post-partum condition in black. The date of birth has been calculated from the H.L. of the pouch young at its first capture, and the approximate duration of pregnancy is indicated by vertical lines. Sexual activity in the non-parous female is indicated by enlargement of the pouch and mammary glands, and such observations, made in the early months of the year at Birdlings Flat, confirmed the reproductive condition deduced from the age of the subsequent pouch young.

Table 5 gives an analysis of the reproductive condition of all the females in the Haurangi Range and Menzies Bay samples. Immature animals are distinguished by an imperforate median vaginal septum and the absence of corpora lutea. In the second row, anoestrus and dioestrus are not distinguished; in April this row includes parous females still in anoestrus, whereas in August and November it represents dioestrous females that no longer have young in the pouch. The fourth row includes all females with corpora lutea that were not macroscopically pregnant nor recently post-partum. Undoubtedly, it includes some females that have undergone an infertile ovulation, but the decline in the relative abundance of this category through April and May suggests that most of the included animals are, in fact, pregnant. The discrepancies in the Haurangi Range and the Menzies Bay totals between the number of post-partum uteri, shown in the sixth row of Table 5, and the number of pouch young, shown in Table 4, are due to the loss of four pouch young collected at Menzies Bay, and because 15 pouch young, recorded in field notes, were not preserved when the Haurangi Range sample was collected. The superscripts in Table 5 denote the number of females in the respective totals that were nulliparous, identified by the presence of an imperforate median vaginal septum. This criterion is, of course, not available after parturition, and consequently no indication of the number of primipari in the post-partum totals is possible.

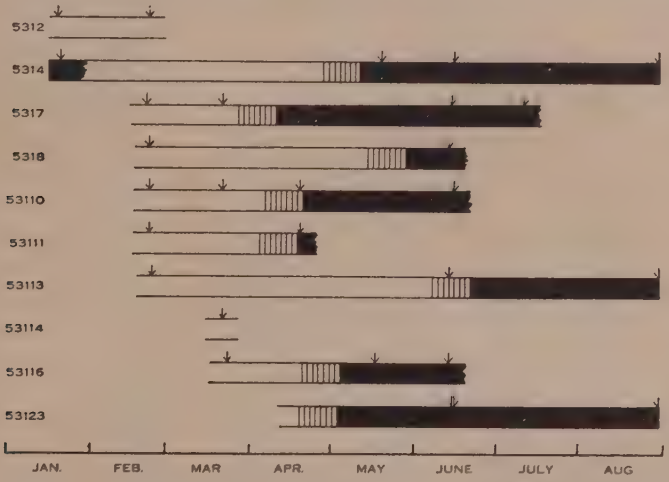

Fig. 4.—Diagrammatic presentation of the individual reproductive histories of 10 adult females observed at Birdlings Flat between January and August 1953, reconstructed from the observed conditions at successive trappings. White represents anoestrus, the vertical lines the approximate duration of pregnancy, and black the time when a pouch young was being carried. Arrows indicate the dates on which observations were made.

Figure 5 represents the relative proportions of the five phases of reproduction at successive periods of time. The percentages are derived from the total females, excluding immature animals which of course do not contribute to the breeding population. The Haurangi Range sample is divided into four subequal groups and the three Menzies Bay samples are treated separately.

The reproductive condition of the Birdlings Flat females observed from January to August 1953 provides the pattern of the breeding season and the larger, dissected samples amplify it. From Figure 4 the onset of breeding activity in March and April is apparent, although the length of the anoestrous period cannot be gauged from these data. The pouch young, carried by No. 5314 in January, and born in October 1952, suggests that for some females the anoestrous period can be quite short. All six females trapped in February were in anoestrus, and four trapped in March were probably also anoestrous, although the pouch of No. 53110 had swollen lips and the nipples were turgid, which suggested an oestrous or pro-oestrous condition. In April, this animal was trapped at full term, as mentioned previously (Section VII (*b*) (ii)), and No. 53111 was trapped with a new-born young. In the subsequent retrapping, all females were carrying young except No. 53113 in June and this specimen had an enlarged pouch and turgid nipples and was subsequently known to have been pregnant at that time. Table 4 and Figure 4 show that the births of pouch young at Birdlings Flat fell between the second week of April and the third week of June. This distribution is in agreement with the distribution of births at Menzies Bay, calculated from the May and August samples. Breeding evidently started a week earlier in the Haurangi Range in 1951 than on Banks Peninsula in 1953. Its full extent in that area, however, cannot be gauged from this sample since the last animals were caught on May 10, and it is evident from the Menzies Bay and Miscellaneous records that a number of young are born after the middle of May and, in fact, that a few are born in nearly all months of the year.

TABLE 5

ANALYSIS OF THE REPRODUCTIVE CONDITION OF THE SAMPLES OF FEMALES FROM HAURANGI RANGE 1951 AND MENZIES BAY 1953

Stage	Haurangi Range				Menzies Bay		
	Apr. 5, 6	Apr. 11-17	Apr. 21-27	May 4, 10	May 10-16	Aug. 15-28	Nov. 3-5
Immature	5^{5}*	1^{1}	0	1^{1}	5^{5}	5^{5}	2^{2}
Anoestrus	1	0	0	0	0	3	4
Oestrus	5^{1}	0	0	0	0	0	0
Ovulation	17	9^{2}	7	3^{1}	2^{2}	1^{1}	0
Pregnant	13^{2}	14^{2}	3^{1}	1^{1}	3^{1}	0	0
Post-partum	2	9	23	26	12	33	1
Total	43	33	33	31	22	42	7
Total less immatures	38	32	33	30	17	37	5

* Superscripts denote the number of nulliparous females in the respective totals.

The Haurangi Range sample is large enough to indicate the reproductive activity of a population during the onset of breeding (see Fig. 5). Of particular note is the very small number of sexually mature females that were not breeding in this sample. This number may be augmented at the beginning of April by the females that have experienced an infertile ovulation (Table 5, 4th row), but by May even this group has declined, so that pregnant and post-partum animals constitute 90 per cent. of the adult female population. The comparable proportion at Menzies Bay in May 1953 was 88 per cent. Figure 5 shows the marked increase in the proportion of post-partum females, from 5 per cent. at the beginning of April to 87 per cent. at the beginning of May, and the corresponding decline in the proportion of pregnant females, and supports the conclusion reached earlier that the gestation period in *Trichosurus* is about 3 weeks. Analysis of the Haurangi Range sample therefore confirms the pattern of reproduction suggested by the Birdlings Flat animals.

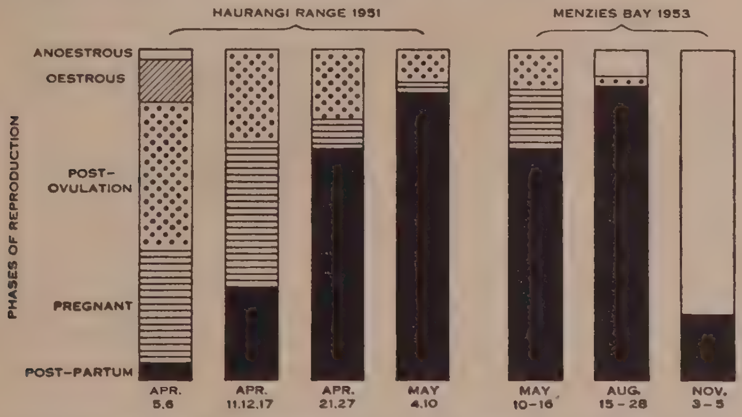

Fig. 5.—The relative proportions of five phases of reproduction at successive periods of time, derived from the sexually mature females in the Haurangi Range and Menzies Bay samples (Table 5). Time along the abscissa and percentage along the ordinate.

Comparing the May samples from Haurangi Range and Menzies Bay (Fig. 5), the proportion of breeding females is about the same in both, but the proportion of post-partum females at Menzies Bay is lower than the Haurangi Range proportion although the sample was collected a week later. This is correlated with the births of pouch young, which occurred earlier at Haurangi Range than at Menzies Bay (see Table 4). Such differences are to be expected when comparing samples obtained in different years and from different localities and do not detract from the fundamental similarity of the pattern of reproduction. Three months later at Menzies Bay, 89 per cent. of the adult females were carrying pouch young and, of the remainder, none was pregnant (Fig. 5). Three parous females were dioestrous and without pouch young. These were all old animals, two in tibial group 2 and one in group 1, and their reproductive condition suggested that they had lost pouch young prematurely. That the proportion of breeding females remained the same from May to August suggests that the mortality rate *in marsupio* during the first 3-4 months is very low or, alternatively, that early losses of pouch young are offset by secondary ovulations. Reynolds (1952) regarded the migration of the new-born young to the pouch as the most critical period of development in *Didelphis*. This conclusion applies, perhaps with greater force, to *Trichosurus*, which is monovular. The occurrence of a post-partum ovulation in this species, and the occasional production of a second embryo as a result, may offset the loss incurred during the migratory phase. Similarly, the regular occurrence of delayed implantation in *Setonix brachyurus* (Sharman 1954) and *Bettongia cuniculus* (Flynn 1930), which are monovular, may have adaptive significance in this context.

In November 1953 five adult females were obtained at Menzies Bay (see Table 5) and all of them had either recently lost pouch young, or the young one was on the parent's back. Four of them were dioestrous and the other had recently given birth, for there was a new-born young in the pouch and also foetal membranes in the uterus. This animal was simultaneously carrying a large kitten on its back, which indicated that it must have ovulated shortly after the older offspring had left the pouch. This is a particularly interesting record as it shows that a female, which breeds in the main season in autumn, can contribute to the second season reported by Bolliger (1940), Wodzicki (1950), and others. Unfortunately the extent of this second season cannot, at present, be determined owing to the lack of an adequate sample in November. Young are evidently born in all months of the year (Table 4) but no indication is afforded by these records of the proportion of females breeding during the spring and summer.

Previous authors have suggested, and the present study does not deny, that *Trichosurus* breeds at the end of the first year. Some indication of the reproductive activity of the young females and of their contribution to the breeding behaviour of the species can be derived from Table 5. For the Menzies Bay samples further information is available, since the animals can be classified according to the degree of ossification of the tibia. In all the samples a few females were immature; in the Haurangi Range sample 3 per cent. were immature, and at Menzies Bay 23 per cent. in May and 13 per cent. in August were immature. The smallness of the latter samples (22 and 42 females respectively) probably exaggerates these proportions, but the difference between the Haurangi Range and Menzies Bay samples may also reflect a real difference in environment, which has affected the survival rate of the young females. The contribution of the young sexually mature females is indicated in Table 5 by superscripts above the respective totals. In the Haurangi Range sample this contribution is general but small, a condition which may be correlated with the small proportion of immature females in this sample. The Menzies Bay samples are smaller but the tibial information allows subdivision of the post-partum totals. Of the 12 post-partum females caught in May, two were in tibial group 3, four in group 2, and six in group 1. In August the corresponding figures were three in group 3, 14 in group 2, and 16 in group 1. Two of the pregnant and both the ovulating females in May were in group 2 and the ovulating female in August was in group 3. It appears from this that the young females were a larger proportion of the breeding population at Menzies Bay than they were at Haurangi Range and the analysis by bone groups shows correlation with the high proportion of immature females found at Menzies Bay. The age structure of a breeding population reflects the past history of the population, as Allee *et al.* (1949) point out. When a population is stable or declining, the young animals constitute a small proportion of the breeding population, but when the population is increasing the proportion of young animals in the breeding population is much higher. At the Menzies Bay station, which covers about 1000 acres, 300 possums were trapped in 1951 and a further 100 in 1952. The consequent loss to the possum population, it is suggested, was reflected in the 1953 samples by a large proportion of young females in the breeding population. Conversely, according to Mr. Pracy, there had been no intensive trapping on the block worked by him in the Haurangi Range for 6 years prior to 1951 when the present sample was collected. The low proportion of young females in the sample from this population appears to reflect an age structure that would be expected in a stable or declining population.

To conclude this section, the present material suggests a pattern of reproduction for *Trichosurus* in which a general anoestrous period in February gives place to increasing reproductive activity through March and April. During May to August, 90 per cent. of the sexually mature females are breeding and the mortality *in marsupio* low. The contribution of the young sexually mature females may vary according to the locality as a result of its effects on the dynamics of the population. By November, the association of the mother and the young is very loose and by this time some females may be breeding again.

IX. MOVEMENTS

The records of 13 adult possums marked and retrapped at Birdlings Flat give some indication of individual movements. These results are presented in Table 6 and Figure 6. Table 6 shows that although more males than females were marked, more females were recaptured and with a greater frequency, but the differences between the sexes are not significant on this small sample. The extent of recorded movement is presented in Figure 6, in which the recapture points are joined together in chronological order. These lines suggest a very restricted range for each animal but, since no traps were set outside the forest, a wider range would not have been detected. That the movements were more extensive was confirmed on August 30, 1953, when the forest and surrounding land were hunted with a dog, and four marked animals were recovered several hundred yards from the study area and only one was recovered on the study area. During live-trapping operations, the traps were always set at night, when the animals were active, whereas on August 30 the animals were hunted in the day-time. This suggests that the possums lay up during the day-time in the surrounding flax and gorse bushes and only moved into the forested area at night, presumably to feed. Nevertheless, they showed a tendency to return to the same restricted area of forest at night, even if they moved considerable distances to their day-time hides. This can be said with some certainty for the females, but the negative records for the males, while not significant because of the small numbers, allow the possibility of wider ranging in this sex.

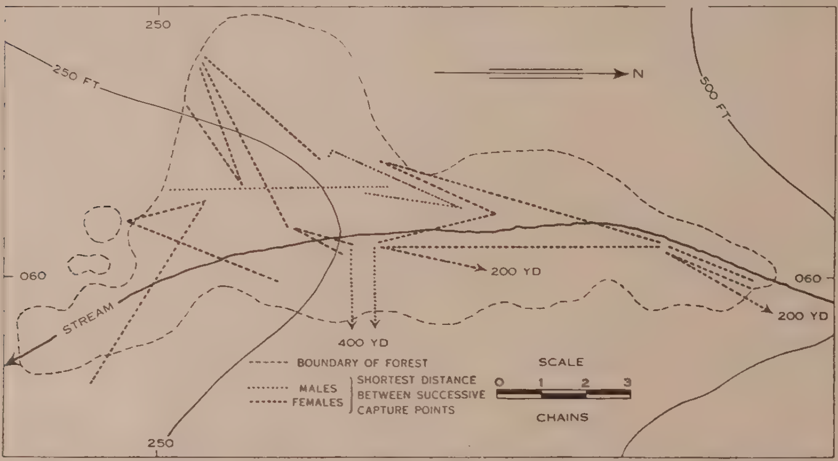

Fig. 6.—Sketch map of the Birdlings Flat study area showing the successive points of capture of the individual possums.

TABLE 6

FREQUENCY OF RECAPTURE OF POSSUMS AT BIRDLINGS FLAT
Males marked, 13; females marked, 10

Number of Times Recaptured	Males		Females	
	Number Caught	Total Recaptures	Number Caught	Total Recaptures
1	4	4	3	3
2	—	—	3	6
3	1	3	3	9
Total	5	7	9	18

X. ACKNOWLEDGMENTS

This paper is condensed from a M.Sc. thesis submitted to the University of New Zealand, and I wish to express my indebtedness to Professor E. Percival, Biology Department, Canterbury University College, Christchurch, who supervised the work; to the members of the Animal Ecology Section, Department of Scientific and Industrial Research, Wellington, especially Dr. K. A. Wodzicki, the Officer-in-Charge, who gave his encouragement practical form by the loan of cage traps and by allowing the manuscript to be prepared in departmental time; to Mr. L. T. Pracy and Mr. T. Riney, Wildlife Branch, Department of Internal Affairs, Wellington, who respectively collected and made available the Haurangi Range material; and finally to Mr. and Mrs. A. Menzies, Menzies Bay, and Mr. A. Birdling, Birdlings Flat, for permission to work on their properties and for their hospitality while doing the work.

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EXPLANATION OF PLATE 1

All the figures except Figure 7 are photomicrographs of sections of the uterus or urogenital sinus stained with Heidenhain's iron haemotoxylin.

Fig. 1.—Uterus of No. 53221 showing the anoestrous condition. × 33.

Fig. 2.—Uterus of No. 53246 at oestrus which, in contrast to Figure 1, shows enlargement of the mucosa and a loosening of the epithelium from the underlying stroma. × 11.

Fig. 3.—Uterus of No. 53260 showing high-power detail of the anoestrous stage: the incipient loosening of the epithelium and the condition of the glandular epithelium. × 280.

Fig. 4.—Uterus of No. 53246 showing high-power detail of the oestrous stage: loose epithelium and the formation of a "secondary epithelium" underneath it. × 280.

Fig. 5.—Uterus of No. 53222 which shows the recently post-partum stage with leucocytes in the loose mucosa, an epithelium consisting of an indistinct layer of cells, and the absence of a loose overlying epithelium. × 280.

Fig. 6.—Uterus of No. 53259 which shows the condition during lactation anoestrus. The mucosa is compact and consists of small glands and blood-vessels and the epithelium, of cuboidal cells, is closely applied to the stroma. × 280.

Fig. 7.—A ventral view of the urogenital organs of No. 51160 with the bladder removed, showing the twin embryos at McCrady's (1938) stage 26 removed from the right uterus and the two active corpora lutea on the right ovary. Note also the enlarged left uterus, which contained no embryo. × *c*. 0.7.

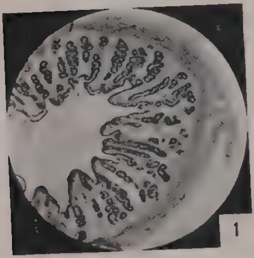
Fig. 8.—Uterus of No. 53219, showing the condition of the epithelial cells of the uterine gland during pregnancy. Note the nuclei at the extreme bases of the cells, in contrast to the condition illustrated in Figure 3. × 280.

Fig. 9.—The urogenital sinus of No. 53260 showing the anoestrous condition. × 7.

Fig. 10.—The same as Figure 9, indicating the unstratified nature of the epithelium at anoestrus. × 196.

Fig. 11.—The urogenital sinus of No. 53246 showing the condition at oestrus, when desquamation of the epithelium occurs. × 7.

Fig. 12.—The same as Figure 11, indicating the nucleated cells of the stratum germinativum (below) and the cornified cells of the stratum corneum (above). × 140.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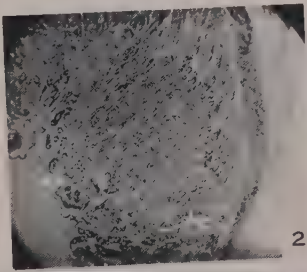
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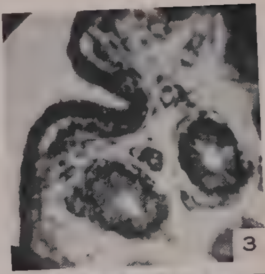
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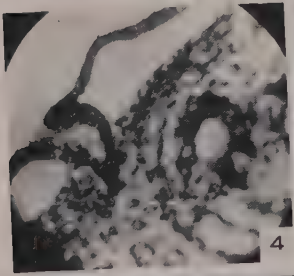
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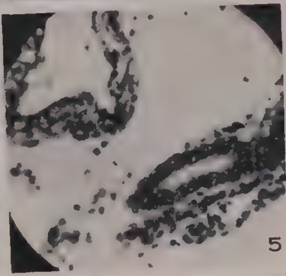
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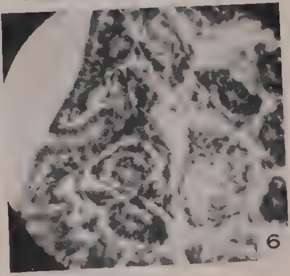
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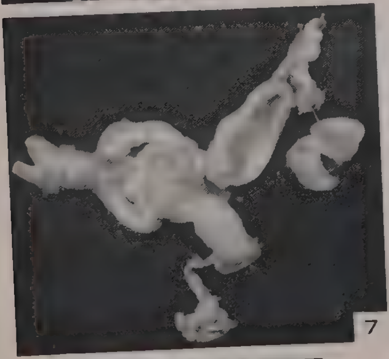
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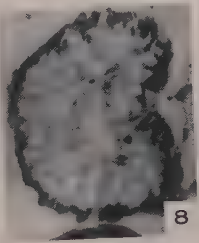
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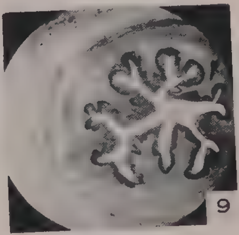
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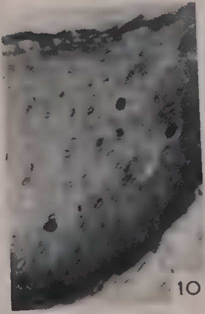
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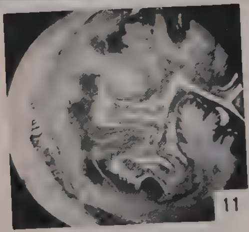
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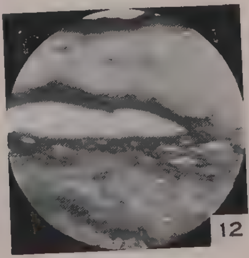
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INFLUENCE OF TEMPERATURE, PHOTOPERIOD, AND FOOD ON THE SPEED OF DEVELOPMENT, LONGEVITY, FECUNDITY, AND OTHER QUALITIES OF THE DIAMOND-BACK MOTH *PLUTELLA MACULIPENNIS* (CURTIS) (LEPIDOPTERA: TINEIDAE)

By A. S. Atwal*

(*Manuscript received December* 20, 1954)

Summary

Larvae of *Plutella maculipennis* (Curtis) were reared on food of different qualities at different temperatures and were exposed during their development to different photoperiods. The plants on which the larvae were reared were also exposed to different photoperiods during their development to see whether this influenced the quality of food for the insect.

It was found that although caterpillars developed more quickly at 25°C than at 18°C, they weighed less at pupation at 25°C than at 18°C, but the ratio of dry matter to water was the same at both temperatures. Exposure of caterpillars to different photoperiods influenced their speed of development. There was an indication that the influence of light was different at different temperatures. The influence of quality of food was more evident. Larvae reared on white or young green leaves of cabbage developed more quickly than those reared on green but mature or senescing leaves; the slower speed of development was associated with a higher death-rate and a lower body weight combined with a higher water content of the pupae. Irrespective of temperature and the quality of the food, females developed more slowly than males and also had more dry matter and a higher liveweight in the pupal stage.

Insects bred at a lower temperature produced more eggs than those at a higher temperature; the difference was thought to be due to a lower body weight in the latter. Photoperiod also influenced fecundity but the effect was not so clear. Caterpillars reared on plants grown in a long photoperiod were more fecund in the adult stage than those reared on plants grown in a short photoperiod, but the difference was not quite significant. Insects reared on white or young green leaves of cabbage laid significantly more eggs than those reared on green but mature leaves. Simarly when larvae were reared on the better quality food they produced more silk, the resulting moths lived longer, and a higher proportion of the males were fertile.

The general conclusion is drawn that for normal activities of *Plutella* a balance of nutrients is required. For the normal activities of the insect body, like healthy development and reproduction, nutrients may be required in certain proportions. If owing to some cause (as probably, with change in season) that proportion is upset, certain abnormalities may appear in the metabolism or form of the insect, such as deformities in wings and shape of body, slow development, reduction or impediment in egg-laying capacity or diapause, etc. In the author's opinion this general conclusion may be a useful hypothesis on which to base further work.

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In the light of the above observations and observations on other insects, the seasonal activity of *Plutella* is discussed. It is stated that although apparently its behaviour and activity seem to be nicely adjusted to seasons, showing a beautiful picture of adaptation, yet the recurrent heavy reductions in numbers which this insect and many other species suffer in the field suggest that the adaptations are not as efficient as may at first sight appear.

I. INTRODUCTION

In the vicinity of Adelaide, S.A., the diamond-back cabbage moth, *Plutella maculipennis* (Curtis) (Tineidae), breeds continuously throughout the year but the rate of increase or decrease in the population fluctuates with the seasons and with the locality. The rate of increase may reflect changes in the speed of development, the longevity, or the fecundity of the individuals in the population. The insects may respond directly to changes in temperature, moisture, light, or food; but the food, consisting of growing plants, may also respond to changes in temperature, moisture, or light so that these factors may also influence the insects indirectly through their food. Also, these climatic factors may not influence the plants and the insects independently; the interactions may be large and complicated. This makes it necessary to use complex factorial experiments to investigate this problem.

There is no diapause in *P. maculipennis*; but for species in which diapause occurs it is known that seasonal changes in temperature, light, or food may result in an entire population's going into diapause at a particular season of the year (Andrewartha 1952). Other species are like *P. maculipennis* in that the progression of the seasons merely results in characteristic fluctuations in the rate of increase of the population; but there may be certain analogies to be drawn between the responses of *P. maculipennis* and those which are associated with the inception of diapause in other species.

In certain aphids variations in photoperiod, temperature, and the quality of the food may cause marked changes in behaviour and fecundity which may also be associated with polymorphic variations in the insects (Marcovitch 1924; Davidson 1929; Ibbotson and Kennedy 1950). The incidence of attacks of the European cornborer *Pyrausta nubilalis* on different varieties of corn varied according to certain physiological differences in the plants as induced by the stage of development, percentage of sucrose, or certain physical characteristics. A high death-rate was associated with slow development and reduced body weight (Bottger and Kent 1931; Ficht 1931, 1936; Polivka 1931). On the same variety of corn the number of larvae that survived was related to the earliness of planting and also to the earliness of silking, which showed the influence due to physiological difference. Larvae of the beetle *Epitrix tuberus* developed better on potato plants than on other host species. The difference in the influence of various diets was believed to be associated with different nutritive values of the foliage (Hill 1946). However, there has been very little work done on the influence of photoperiod on the biology of insects (except in relation to diapause). The influence of plants in different physiological conditions on the fecundity, longevity, and speed of development of certain insects has been observed and commented on rather more frequently, but in this field also there has been comparatively little experimental work done.

This paper describes a number of experiments with *P. maculipennis* in which the larvae and adults were kept at various temperatures and exposed to various photoperiods. The larvae were reared on the leaves of cabbages which varied in age, and in the photoperiod and temperature experienced during growth. The speed of development and longevity of the larvae and the fecundity and longevity of the adults were measured.

II. MATERIALS AND METHODS

Most of the eggs for the experiments were laid by moths reared in the laboratory—perhaps during previous experiments. When this source was inadequate, especially in the spring, pupae or adult moths were collected from cabbage fields in the Waite Institute grounds or suburbs of Adelaide, mostly from Findon and Montacute.

Moths collected from the fields were kept in batches of 20-25, males and females together, in cylindrical specimen tubes 5 by 1 in. containing a piece of green cabbage leaf and corked or covered with a piece of muslin cloth at the mouth. They laid eggs quite readily on the piece of leaf inside or even on the cylindrical walls of the tubes. The eggs could be removed easily with a camel hair brush soaked in a dilute solution of sodium hypochlorite. Sometimes the water transpired by the leaf would condense on the sides of the tube and drown the moths or stick them to the glass by their wings so that they died. Except when this happened the moths laid plenty of eggs and it was possible to get enough for each experiment of nearly the same age, varying within 24-72 hr. When the eggs were obtained from material left over from the previous experiment they were usually from single females which had been kept with two or three males in specimen tubes 2 by $\frac{13}{16}$ in.

Moths were offered dilute honey solution by soaking a plug of cotton wool in it and sticking that to the inside of a cork at the mouth of a tube. Since the moths are negatively geotropic and the specimen tubes in which they lived stood upright they reached the food quite quickly. Moths did not hesitate to lay eggs even in the absence of honey solution or water, though at high temperatures and in a dry atmosphere they died very quickly if some watery food were not provided.

Petri dishes containing eggs on damp filter-papers were placed in air-tight Fowler glass jars. At the bottom of the jar another damp filter-paper was placed; this provided sufficient humidity inside without much risk of water condensing on the glass. The jars were then placed in incubators which maintained the temperature constant within ±0.2°C.

Ordinarily eggs were incubated at the same temperatures used subsequently for rearing the larvae, but sometimes eggs laid late were brought from a lower to a higher temperature to quicken the development so that they could be hatched at or near the same day as the ones laid earlier. This had to be done particularly in those seasons when enough moths could not be collected from the field. In these cases caterpillars from each batch of eggs were distributed equally and at random among all the treatments.

Such extremes of temperatures as 11 and 27°C appeared to have a harmful influence on the normal growth of caterpillars. Temperatures ranging from 17 to 25°C were found to be quite favourable and most of the experiments were done at temperatures within this range.

The eggs of *Plutella* are fairly resistant to excessive water around them and in dry atmospheres too they can remain alive for a limited time. Eggs which are nearly ready to hatch may be stimulated to hatch by dryness. On the other hand eggs which are not quite ready to hatch may be hampered in their development or killed by exposure to dryness. Special care, therefore, needs to be taken to keep the filter-paper just damp, particularly as the time of hatching approaches. Eggs were placed on the filter-papers either singly or in batches; they developed and hatched equally well in either case. Since the newly hatched caterpillars are very small they can be drowned in a slight excess of water that might be ignored on a filter-paper, or even in the microscopic droplets of water sticking to the inside of jars; it is therefore very important to control the humidity in the jars where the eggs are hatching.

In different experiments as mentioned later, newly hatched caterpillars were collected every 6-8 or 12 hr and those in each lot were distributed at random among all the treatments. During these intervals of time no food was given to the larvae and this did them no harm that could be detected, but if they were allowed to roam about for more than 12 hr they appeared to have exhausted themselves. If larvae which had so exhausted themselves were later transferred to food, either they could not appreciate its presence or they failed to mine in despite repeated attempts to bite; and consequently, they died. In the presence of excessive dampness inside the hatching jars, however, they became exhausted, or drowned, far more quickly.

Caterpillars were reared in glass specimen tubes 2 by $\frac{13}{16}$ in., corked on top. At the bottom, circles of filter-paper were spread and were irrigated with a drop of water every morning for the first few days of the caterpillar's life so as to keep the pieces of cabbage leaf inside turgid. A piece of cabbage leaf $\frac{3}{4}$ by $\frac{3}{4}$ in. for a larva was considered of a reasonable size for a start. As the larvae grew and the chance of losing them was reduced the size of the leaf was increased. In all the experiments in which food was a variable, the pieces of cabbage leaves were thoroughly mixed before they were distributed among the caterpillars. Any unhealthy or abnormal-looking (virus-attacked) leaves were rejected. Midribs were not given.

When newly emerged larvae were placed on pieces of cabbage leaf most of them had disappeared inside the leaf within 2 hr. Most of the larvae entered from the under surface but a few were able to bore through the upper surface. During the first two instars they feed inside mines, changing to a new one after the first moulting. Quite commonly the first exuviae were observed outside the mines.

The first change of food was regulated in such a way that at any one temperature it was made after the first moulting to avoid injury to the small first instar caterpillars. For example at 25-22, 20, or 18-17°C food was changed on the third, fourth, or fifth day respectively. However, it was changed earlier if it became yellowish before that time. Subsequently food was changed every other day and at the same time tubes were also cleaned. In certain circumstances when the food given was undesirable, many caterpillars died and their deaths seemed to be associated with certain species of bacteria and moulds.

In recording the results the prepupal stage was assumed to begin when the caterpillars started spinning, and the pupal stage when the last larval skin was pushed back towards the anal end of the silken cocoon. As mentioned in the tables, the prepupal life was added either to the larval or pupal life. When the duration of the life of larvae or pupae was being measured, observations were taken after very 8 or 12 hr as indicated in Section III.

The pupae were left in cleaned tubes, with a little piece of leaf to provide humidity, and were not separated out of their cocoons unless they were neded for weighings.

Sexes could be differentiated as easily in the adults as in the pupal stages (Robertson 1939, p. 345). The female moths were recognized by a small tuft of hair at the end of the abdomen, and males by the two distinct valves. In experiments where the fecundity of a female was being measured two or three males were placed in the tube with each female because some males were sterile. The males usually included one which had been bred in the laboratory and others collected from the field. This increased the chance that there would be at least one fertile male in the tube with the female. If any of the females failed to lay eggs her males were replaced by fresh ones to ensure that a fertile male was always available.

III. RESULTS

(*a*) *Experiment* 1: *Influence of Cabbage Leaves of Different Ages at two Temperatures on Some Characteristics of Males and Females*

A factorial experiment was designed in which larvae were reared at two temperatures and on four different foods, viz.:

Temperature.—18 and 25°C.

Food.—(1) White leaves from the heart of a cabbage plant, P_1.
(2) Green leaves, vigorously growing, from another cabbage plant P_2 (2 ft away from P_1 in the field).
(3) Mature leaves from plant P_1.
(4) Old senescent leaves from plant P_1.

Sex.—The influence of these variables was studied on males and females separately.

Eggs were taken from moths reared in the laboratory. Each of the treatments shown above was started with 35 caterpillars hatched within 8 hr on April 8, 1952, and it was expected that some of them would die while being reared. All the young larvae on mature and old senescent leaves failed to mine in and died within 48 hr. On April 10, therefore, a fresh lot of larvae was started for these sets of treatments. They were allowed to feed on tender green leaves during their first instar, and then changed to the experimental foods. Even then none survived on the old senescent leaves.

TABLE 1

MEAN LENGTH OF LARVAL LIFE (HATCHING TO PUPATION) IN DAYS AT DIFFERENT LEVELS OF TEMPERATURE AND QUALITY OF FOOD

Mean based on 12 observations

Food	18°C		25°C		Both Sexes		Both Temps.		Mean
	Male	Female	Male	Female	18°C	25°C	Male	Female	
White leaves	16.6	17.3	8.4	8.6	16.9	8.5	12.5	12.9	12.7
Green leaves	16.5	16.8	8.4	8.8	16.7	8.6	12.4	12.8	12.6
Mature leaves	21.3	23.0	9.2	9.6	22.2	9.4	15.2	16.3	15.8
S.D. ±		0.30(a)			0.21(b)		0.21(b)		0.15(c)
Mean	18.1	19.0	8.7	9.0	18.6	8.8	13.4	14.0	13.7
S.D.±		0.17(d)			0.12(e)		0.12(e)		

		$P = 0.05$	$P = 0.01$	$P = 0.001$
Min. significant difference;	(a)	0.8	1.1	1.4
	(b)	0.6	0.8	1.0
	(c)	0.4	0.5	0.7
	(d)	0.5	0.6	0.8
	(e)	0.3	0.4	0.6

Analysis of variance: temperature, $P < 0.001$; food, $P < 0.001$; sex, $P < 0.001$; interaction of food and temperature, $P < 0.001$; none of the other interactions significant

To measure the duration of larval life, observations were made twice a day at 9 a.m. and 5 p.m. Measurements of the liveweight of pupae were done 24 hr after pupation at 25°C and 48 hr after at 18°C, to let the chrysalis become reasonably hard in order to avoid injury when the cocoon was removed.

To get the weight of dry matter, pupae were dried in the oven at 102°C, the first reading being taken after 24 hr and the second after 48 hr.

TABLE 2

MEAN LIVEWEIGHT OF PUPA (MG) AT DIFFERENT LEVELS OF TEMPERATURE AND QUALITY OF FOOD

Mean based on 12 observations

Food	18°C		25°C		Both Sexes		Both Temps.		Mean
	Male	Female	Male	Female	18°C	25°C	Male	Female	
White leaves	6.67	8.13	4.86	5.54	7.40	5.20	5.76	6.83	6.30
Green leaves	6.62	8.41	4.46	5.55	7.51	5.01	5.54	6.98	6.26
Mature leaves	6.17	6.15	4.15	4.51	6.16	4.33	5.16	5.33	5.24
S.D. ±		0.183$^{(a)}$			0.129$^{(b)}$		0.129$^{(b)}$		0.091$^{(c)}$
Mean	6.49	7.56	4.49	5.20	7.02	4.84	5.49	6.38	5.93
S.D.±		0.106$^{(d)}$			0.075$^{(e)}$		0.075$^{(e)}$		

		$P = 0.05$	$P = 0.01$	$P = 0.001$
Min. significant difference:	(a)	0.51	0.67	0.85
	(b)	0.36	0.47	0.60
	(c)	0.25	0.33	0.43
	(d)	0.29	0.39	0.49
	(e)	0.21	0.27	0.35

Analysis of variance: temperature, $P < 0.001$; food, $P < 0.001$; sex, $P < 0.001$; interactions: food × temperature, $P < 0.05$; sex × temperature, N.S.; sex × food, $P < 0.001$

TABLE 3

MEAN WEIGHT (MG) OF SILK (COCOON) AT DIFFERENT LEVELS OF TEMPERATURE AND QUALITY OF FOOD

Mean based on 12 observations

Food	18°C		25°C		Both Sexes		Both Temps.		Mean
	Male	Female	Male	Female	18°C	25°C	Male	Female	
White leaves	0.222	0.257	0.167	0.174	0.239	0.170	0.194	0.215	0.205
Green leaves	0.225	0.258	0.164	0.196	0.242	0.180	0.195	0.227	0.211
Mature leaves	0.220	0.212	0.137	0.148	0.216	0.142	0.178	0.180	0.179
S.D. ±		0.0106$^{(a)}$			0.0075$^{(b)}$		0.0075$^{(b)}$		0.0053$^{(c)}$
Mean	0.222	0.242	0.156	0.173	0.232	0.164	0.189	0.207	0.198
S.D.±		0.0061$^{(d)}$			0.0043$^{(e)}$		0.0043$^{(e)}$		

		$P = 0.05$	$P = 0.01$	$P = 0.001$
Min. significant difference:	(a)	0.029	0.039	0.049
	(b)	0.021	0.027	0.035
	(c)	0.015	0.019	0.025
	(d)	0.017	0.022	0.029
	(e)	0.012	0.016	0.020

Analysis of variance: temperature, $P < 0.001$; food, $P < 0.001$; sex, $P < 0.01$. None of the interactions significant

The silk (cocoon without last larval cuticle) was weighed on a torsion balance calibrated to 0.01 mg.

Summaries of the results are given in Tables 1-5. The standard deviations (S.D.) refer to all the quantities within a particular "box" within a table.

Caterpillars developed significantly more slowly on mature leaves than on young green and white leaves (Table 1), and more slowly at 18°C than at 25°C. Females developed more slowly than males.

Pupae did not become so heavy on mature leaves as on white and young green leaves (Table 2). Females were heavier than males on the whole, but on mature leaves their weight was reduced relatively more than that of the males. With both sexes reared on mature leaves the reduction in weight, compared with those reared on white and young green leaves, was relatively greater at 18°C than at 25°C.

TABLE 4

MEAN WEIGHT OF DRY MATTER OF PUPA (MG) AT DIFFERENT LEVELS OF TEMPERATURE AND QUALITY OF FOOD

Mean based on five observations

Food	18°C		25°C		Both Sexes		Both Temps.		Mean
	Male	Female	Male	Female	18°C	25°C	Male	Female	
White leaves	0.165	0.226	0.120	0.160	0.195	0.140	0.142	0.193	0.168
Green leaves	0.167	0.249	0.113	0.169	0.208	0.141	0.140	0.209	0.174
Mature leaves	0.160	0.169	0.104	0.109	0.164	0.106	0.132	0.139	0.135
S.D.±	0.0102(a)				0.0072(b)		0.0072(b)		0.0051(c)
Mean	0.164	0.215	0.112	0.146	0.189	0.129	0.138	0.180	0.159
S.D.±	0.0059(d)				0.0042(e)		0.0042(e)		

Min. significant difference:	$P = 0.05$	$P = 0.01$	$P = 0.001$
(a)	0.029	0.039	0.051
(b)	0.021	0.027	0.036
(c)	0.015	0.019	0.025
(d)	0.017	0.022	0.029
(e)	0.012	0.016	0.021

Analysis of variance: temperature, $P < 0.001$; food, $P < 0.001$; sex, $P < 0.001$; interaction sex × food, $P < 0.001$; none of the other interactions significant

At 18°C more silk was produced than at 25°C (Table 3). On mature leaves less silk was produced but there was no difference between young green and white leaves. Females made heavier cocoons than males.

For dry weight of pupa (Table 4) the same treatments were significant as in liveweight of pupa (Table 3), but the interaction food × temperature was not significant, which suggests that the relatively greater influence of food on liveweight at 25°C than at 18°C may have been due largely to difference in the water content of the body, unless it was due to chance; the interaction was significant only at the 5 per cent. level.

On mature leaves the ratio of liveweight to dry matter in pupae was higher owing to a greater percentage of water in their bodies (Table 5). Males had a higher ratio than females, which means the latter were more solidly built.

TABLE 5

MEAN RATIO OF LIVEWEIGHT TO DRY MATTER IN THE PUPA AT DIFFERENT LEVELS OF TEMPERATURE AND QUALITY OF FOOD

Mean based on five observations

Food	18°C		25°C		Both Sexes		Both Temps.		Mean
	Male	Female	Male	Female	18°C	25°C	Male	Female	
White leaves	4.06	3.52	3.92	3.47	3.79	3.70	3.99	3.50	3.75
Green leaves	3.85	3.70	3.82	3.53	3.78	3.67	3.83	3.62	3.72
Mature leaves	4.11	3.84	4.10	3.92	3.97	4.01	4.10	3.38	3.99
S.D.±	0.107$^{(a)}$				0.075$^{(b)}$		0.075$^{(b)}$		0.053$^{(c)}$
Mean	4.00	3.69	3.95	3.64	3.85	3.79	3.98	3.66	3.82
S.D.±	0.062$^{(d)}$				0.044$^{(e)}$		0.044$^{(e)}$		

		$P = 0.05$	$P = 0.01$	$P = 0.001$
Min. significant difference:	(a)	0.30	0.41	0.53
	(b)	0.22	0.29	0.38
	(c)	0.15	0.19	0.25
	(d)	0.18	0.23	0.31
	(e)	0.12	0.17	0.22

Analysis of variance: sex, $P < 0.001$; food, $P < 0.01$; none of the other treatments or interactions significant

(*b*) *Experiment 2: Influence of Quality of Food and Photoperiod at Different Temperatures on Fecundity and Speed of Development*

Caterpillars were reared at two temperatures on pieces of leaf from cabbage plants grown in the field in two photoperiods. Further, in the incubators, growing larvae were exposed to electric light during the daytime, for either 9 or 15 hr. Thus the design of the experiment was factorial and treatments were:

Temperature.—18 and 21°C.

Food.—(1) Cabbages grown in long-day period (15 hr of daylight).
(2) Cabbages grown in short-day period (9 hr of daylight).

Exposure to light.—9 and 15 hr (in incubators).

The experiment was started with caterpillars hatched within 6 hr. An extra set of caterpillars was reared on food (1), in 15 hr of exposure to light at each temperature. In the adult stage those reared at 18 were brought to 21°C and vice versa. The fecundity of those moths was compared with that of those reared and kept at the same temperatures throughout the life cycle, because it was thought that an abrupt change of temperature at the beginning of the adult stage might influence the fecundity of the moths.

The two types of plants were grown in six little plots of five plants each in the field; to allow for differences in the fertility of the soil the plots were distributed at random. Since the plants were grown during the summer months of November and December, those to be grown in a short-day period were covered by light-proof wooden boxes during the night and for part of each day. The boxes, 18 by 18 by 16 in., were lined with "Sisalkraft" and were painted white on the outside to reflect the sun's rays and black on the inside to help provide complete darkness (Fig. 1). Three predetermined plots were covered by such boxes each evening at 5 p.m. and uncovered next morning at 9 a.m. To ensure total darkness, every evening after inverting the boxes their edges were sealed with soil all round. Plants in the other three plots growing in 15 hr of daylight were covered with similar boxes having one wall made of glass. These boxes were placed over the plants and removed at the same time as the others so as to provide like conditions of temperature for the plants growing under them; the glass walls were kept facing the south to prevent direct rays of the sun from penetrating inside the boxes and thus possibly raising the temperature.

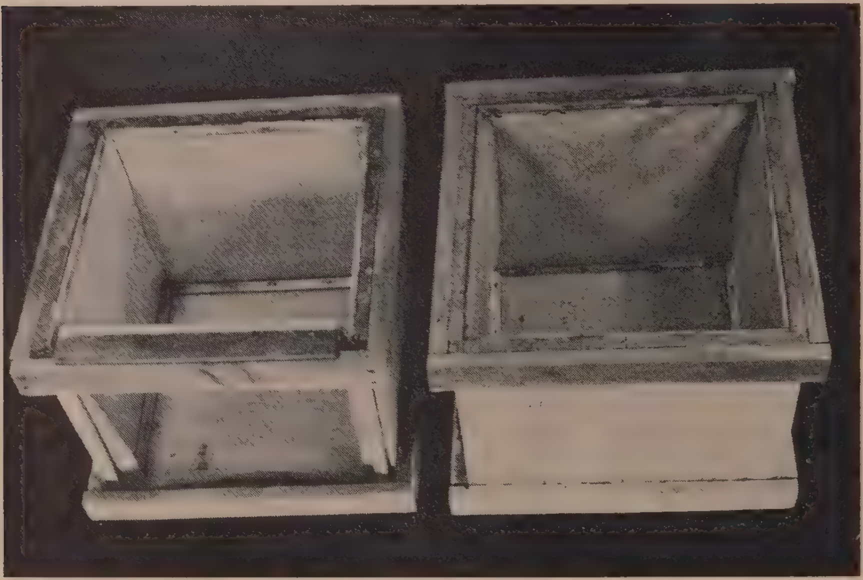

Fig. 1.—Wooden boxes used to control photoperiod on cabbage plants grown in the field (experiment 2).

Table 6

DURATION OF LARVAL AND PUPAL LIFE AND FECUNDITY OF MOTHS AT DIFFERENT LEVELS OF TEMPERATURE, PHOTOPERIOD, AND QUALITY OF FOOD

Variable number of observations; speed of development mean of 20 observations

A. Results

Treatments			Fecundity		Speed of Development	
Food Grown in	Caterpillars Reared in		No. of Females	Av. No. of Eggs	Length of Larval Life (days)	Length of Prepupal + Pupal Life (days)
	Photo-period (hr/day)	Temp. (°C)				
Long day	9	18	15	175	15.3	10.4
Short day	9	18	19	193	14.6	10.3
Long day	15	18	15	229	14.0	10.1
Short day	15	18	18	208	14.2	10.2
Long day	9	21	12	157	10.3	7.4
Short day	9	21	15	125	10.4	7.1
Long day	15	21	14	191	10.6	7.3
Short day	15	21	20	150	10.6	7.2

B. Summary of Effects

Effect	No. of Eggs per Moth	Length of Larval Life (days)	Length of Prepupal + Pupal Life (days)
Food (short day — long day)	—19.0	—0.1	—0.1
Photoperiod (15—9 hr)	32.0*	—0.3*	—0.1
Photoperiod × food	—12.0	0.3*	0.1
Temperature (21—18°C)	—45.5**	—4.0***	—3.0***
Temperature × food	—17.5	0.2	—0.1
Temperature × photoperiod	—2.5	0.5***	0.1
Temperature × food × photoperiod	7.5	—0.3*	—0.01
Mean	179	12.5	8.7
S.D.±	13.89	0.16	0.10
Min. significant effects:			
$P = 0.05$	27.2	0.3	0.20
$P = 0.01$	35.8	0.4	0.26
$P = 0.001$	45.7	0.5	0.33

C. Details of Interactions (length of larval life)

Photoperiod × Food			
Food	Photoperiod		Mean
	9 Hr	15 Hr	
Short day	12.9	12.3	12.6
Long day	12.5	12.5	12.5
Mean	12.7	12.4	

Temperature × Photoperiod			
Temperature (°C)	Photoperiod		Mean
	9 Hr	15 Hr	
18	14.9	14.1	14.5
21	10.4	10.6	10.5
Mean	12.7	12.4	

The light was first controlled about 2 weeks after the seedlings had been transplanted; and 6 weeks later the caterpillars were first fed on them. Throughout the experiment plants remained growing under the same conditions. For feeding, leaves were picked at random and cut into square pieces which were thoroughly mixed before being distributed among the various treatments.

The caterpillars used were hatched from eggs collected in experiment 3; as hatching started, after every 6 hr they were distributed among all the treatments in equal numbers, so that within 24 hr each treatment was started with 60 larvae. Two caterpillars were reared in each specimen tube.

In order to estimate the duration of larval and pupal life 20 individuals from each treatment were selected at random, and were observed every 8 hr. Eggs of all the females that reached the adult stage were counted every day; there were therefore a variable number of observations in the different treatments. Each female moth was provided with two males, though not necessarily the same two, throughout her life.

TABLE 7

INFLUENCE OF CHANGE OF TEMPERATURE ON FECUNDITY

Variable number of observations

Food Grown in	Larvae Reared		Adults Reared:	Fecundity of Female Moths		
	Photoperiod (hr)	Temperature (°C)	Temperature (°C)	No. Laying Eggs	Av. No. of Eggs	S.D.±
Long day (15 hr)	15	18	18	15	229	20.02
Long day (15 hr)	15	18	21	14	152	20.72
Long day (15 hr)	15	21	18	9	184	25.85
Long day (15 hr)	15	21	21	14	191	20.73

The results are set out in Tables 6*A*, 6*B*, 6*C*, and 7. In Table 6*B* and similar subsequent tables the "summary of effects" is given in the form described by Yates (1937). The magnitudes of the "main effects" and the interactions are indicated by positive or negative deviations in the appropriate columns; and the significance is indicated by asterisks, thus: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

The only treatment in Table 7 that gave a significant result was that of raising the temperature from 18 to 21°C; the difference was significant at the 1 per cent. level.

At 18°C more eggs were produced than at 21°C; the difference, 46 eggs per female, was significant at the 1 per cent. level. Moths from caterpillars which were reared in a 15-hr photoperiod produced on an average 32 more eggs than those reared in a 9-hr photoperiod. This difference was significant at the 5 per cent. level. However, the larvae required on an average 0.3 day longer to complete their development at the shorter photoperiod. Larvae feeding on plants grown in a 9-hr photoperiod developed more slowly when exposed to 9 hr of light per day than when exposed to 15 hr (this interaction was significant at the 5 per cent. level), but those feeding on plants grown in a 15-hr photoperiod developed equally quickly whether they were exposed to 9 or 15 hr of light each day in the incubator.* At 21°C the shortening of life was not as much in the 15-hr photoperiod as in the 9-hr; or conversely, at 18°C the lengthening of life was not as great in the 9-hr photoperiod as in the 15-hr, the interaction being significant at the 1 per cent. level. Apart from temperature no other factor influenced the length of pupal life. Those

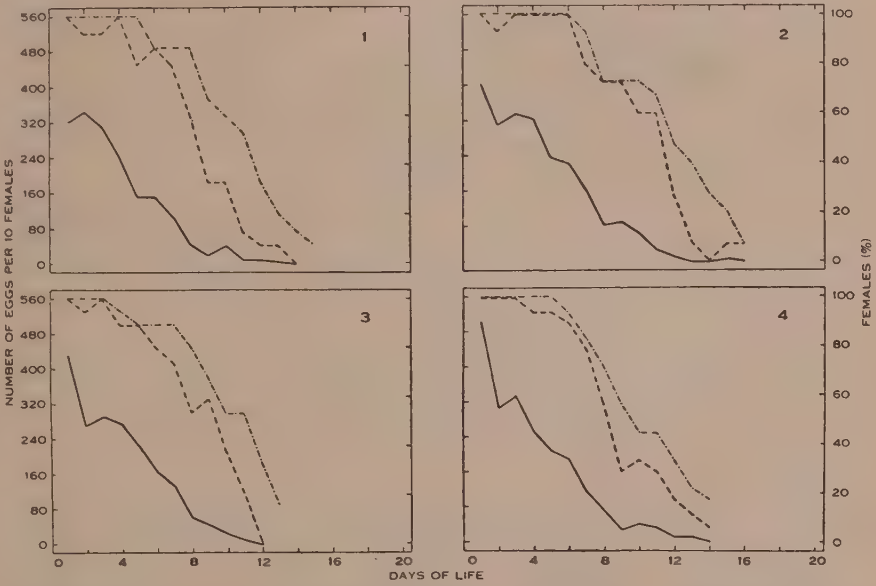

Fig. 2.—Fecundity and oviposition behaviour of *Plutella* at different levels of temperature, photoperiod, and quality of cabbage leaves (experiment 2). ——— Number of eggs; ---- egg-laying females (% of original number); -.-.-. females surviving (% of original number). Graphs 1 and 2, caterpillars reared in 9-hr photoperiod: 1, food grown in long day; 2, food grown in short day. Graphs 3 and 4, caterpillars reared in 15-hr photoperiod: 3, food grown in long day; 4, food grown in short day. All caterpillars reared at 18°C.

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* Plants grown at a controlled photoperiod in the field showed appreciable response to this treatment within 6 weeks; towards the end of this period those grown in 9 hr of daylight were 3-4 in. high whereas those grown in 15 hr were 7-9 in., which showed that long photoperiod favoured plant growth.

caterpillars which were reared at 18°C and then brought to 21°C in the adult stage laid fewer eggs than those which were reared and kept at 18°C throughout their life cycle. Figure 2 shows the graphs of oviposition behaviour and longevity of female moths under different treatments.

(c) *Experiment* 3: *Influence of Temperature and Photoperiod on Speed of Development and Fecundity*

Caterpillars were reared at 20 and 24°C in 15 and 9 hr of exposure to electric light (40 W) in incubators.

For this experiment moths were caught in the fields under early spring cabbages and swede crops. They laid eggs at 20°C which were incubated at 24°C. The hatching of the larvae was spread over 4 days. Each larva was placed on the appropriate food within 6 hr of hatching. They were reared individually in separate tubes.

Marked differences were observed in the speed of development between larvae hatched on different days. These differences were therefore removed from the estimate of error. Owing to unequal survival, there was a varying number of replications in different treatments with respect to measurement of the length of life.

Each female on emergence was provided with three males, one from the experiment and two from the fields collected at the pupal stage.

Caterpillars that hatched on October 26 and 28 developed significantly more quickly than those hatching on October 24 and 25 (Table 8).

Remarks

(1) The number of caterpillars started in each treatment on different days were: 18 on October 24, 26 on October 25, 6 on October 26, and 15-20 (varying in different treatments) on October 28. The caterpillars that hatched on October 24 were given tender green leaves from a plant (say No. 1) of the same stock as had been used in experiment 8 (there was very high mortality then, suspected to be due to undesirable food). In their second instar white leaves from the heart of another plant (say No. 2) from a different stock (probably a different variety) were given to them. On the other three dates this food from plant No. 2 was given to larvae from the start. After this plant was eaten up another one of the same variety was used for the rest of the larval period in all treatments. These three plants of cabbage were growing in the field within 2 ft of each other. As may be seen from Table 8A, there was no difference in the length of life of the caterpillars hatched on October 24 and 25. The greatest difference in the food occurred between these two dates, whereas there was no difference in the food given to those hatching on October 25, 26, and 28. It therefore seems likely that the difference in the speed of development of the larvae which hatched on the first two days and those which hatched on the last two days must be due to some other cause.

(2) On October 24 when the experiment was started, electric lights were turned on in the incubators and from then on the developing eggs

TABLE 8

AVERAGE LENGTH OF LARVAL + PUPAL LIFE (DAYS) AT DIFFERENT LEVELS OF TEMPERATURE AND PHOTOPERIOD

Variable number of observations

A. Results

Hatched on	24°C				20°C				Weighted Mean
	Photoperiod 15 Hr		Photoperiod 9 Hr		Photoperiod 15 Hr		Photoperiod 9 Hr		
	No. of Insects	Av. Life	No. of Insects	Av. Life	No. of Insects	Av. Life	No. of Insects	Av. Life	
Oct. 24	3	14.6	2	17.9	3	21.1	3	20.6	18.6
Oct. 25	4	15.8	2	16.2	4	19.8	4	20.1	18.2
Oct. 26	5	12.6	6	12.3	4	16.3	4	15.9	13.9
Oct. 28	9	13.3	11	12.7	7	16.6	12	16.0	14.6
Weighted mean		13.8		13.4		17.9		17.3	15.7

B. Summary of Effects (length of larval + pupal life)

Treatment		Hatched on				
Temperature (°C)	Photoperiod (hr)	Oct. 24	Oct. 25	Oct. 26	Oct. 28	Mean
24	15	14.6	15.8	12.6	13.3	14.1
24	9	17.8	16.2	12.3	13.0	14.8
20	15	21.1	19.8	16.3	16.3	18.4
20	9	20.6	20.1	15.9	16.0	18.2
Mean		18.5	18.0	14.3	14.6	16.4
Effects of:						
Temperature (24—20°C)		—4.6	—4.0	—3.6	—3.0	—3.8
Photoperiod (15—9 hr)		—1.4	—0.4	0.4	0.3	—0.2
Interaction: (24—20°C) × (15—9 hr)		—1.8	0	0	0	—0.4
S.D. of effects ±		0.94	0.86	0.71	0.50	0.39
Min. significant difference (65 d.f.):						
$P = 0.05$		1.9	1.7	1.4	1.0	0.8
$P = 0.01$		2.5	2.3	1.9	1.3	1.0
$P = 0.001$		3.2	3.0	2.5	1.7	1.3

C. Comparison between Larvae which Hatched on Specified Dates

Date of Hatching (1952)	Average Life (days)	S.D. ±	Min. Significant Difference		
			$P = 0.05$	$P = 0.01$	$P = 0.001$
Oct. 24 and 25	18.2	0.90			
Oct. 26 and 28	14.4	0.62			
Difference	3.8	1.10	2.2	2.9	3.8

Analysis of variance: temperature, $P < 0.001$; dates of hatching, $P < 0.001$; no other main effect or interaction significant lying inside remained in continuous light. Thus the eggs that hatched on October 25 remained in light for 24 hr; those on October 26 for 48 hr; and those on October 28 during their entire embryonic development.

(*d*) *Experiment* 4: *Influence of Photoperiod during Incubation and Rearing on Speed of Development*

In experiment 3, caterpillars hatched on October 26 and 28, 1952, developed more quickly than those hatched on October 24 and 25, and it was thought that this might have been due to the exposure of the eggs to light for different lengths of time (Tables 8*A* and 8*B*). This experiment was repeated on the same dates the next year (caterpillars hatched on October 23, 24, and 25, 1953) to see if photoperiod during the incubation of eggs from overwintering moths had any influence on their subsequent development in the larval period.

TABLE 9

DURATION OF LIFE IN DAYS (HATCHING TO PUPATION) AT DIFFERENT PHOTOPERIODS DURING INCUBATION AND REARING AT 17°C

Mean based on 25 observations

Rearing Photoperiod	Incubation Photoperiod 9 Hr	 15 Hr	Mean
9 hr	17.7	18.0	17.8
15 hr	15.3	15.6	15.4
S.D.±	0.23(a)		0.16(b)
Mean	16.5	16.8	16.6
S.D.±	0.16(b)		

	$P = 0.05$	$P = 0.01$	$P = 0.001$
Min. significant difference: (a)	0.6	0.9	1.1
(b)	0.5	0.6	0.8

Analysis of variance: treatment during rearing, $P < 0.001$; treatment during incubation, not significant

Third instar caterpillars were collected from the field (Waite Institute) and reared in the laboratory at 17°C. As moths they laid eggs at the same temperature. The eggs were incubated at 17°C, half of them being exposed to 9 hr of electric light (1 ft away from a "Mazda" 40-W globe) each day, and the other half to 15 hr of light daily. As they hatched, the larvae from both lots were reared at 17°C in a 9-hr and a 15-hr photoperiod each day.

The caterpillars hatched only during exposure to light, and within 2-4 hr of their hatching they were distributed at random among the respective treatments. They were reared individually on young green leaves of cabbage in glass specimen tubes. To note the time of pupation they were observed every 8 hr.

The larvae from eggs exposed to 15 hr of light each day during incubation developed at the same speed as those from eggs exposed to 9 hr (Table 9); but the larvae exposed to a 15-hr photoperiod while rearing developed more quickly than those exposed to a 9-hr photoperiod. The difference was significant at the 0.1 per cent. level.

(*e*) *Experiment* 5: *Influence of Cabbage Leaves in Different Stages of Development on Fecundity*

Caterpillars were reared at a constant temperature of 17°C on three types of food:

A, White leaves from the heart of a cabbage plant, say P_1, growing in the field.

B, Green leaves vigorously growing, from another plant, P_2, 2 ft away.

C, Mature leaves from plant P_1.

These foods were either given during the entire larval life or were changed in different instars (Table 10).

TABLE 10

COMBINATIONS OF TREATMENTS IN EXPERIMENT 5

Treatment No.	Foods Given in Larval Instars			
	1st	2nd	3rd	4th
1	A	A	A	A
2	A	A	A	B
3	A	A	B	B
4	B	B	B	B
5	B	B	B	C
6	B	B	C	C
7	A	A	A	C
8	A	A	C	C

The caterpillars used were hatched from eggs laid by moths of experiment 1. The larvae of any one treatment were reared together in a Fowler glass jar. On emergence 10 female moths from every treatment (except treatment No. 5 with seven replications) were provided with two males each, one from the experiment and one from the field. Eggs laid by them were counted every day.

Caterpillars fed on white leaves laid more eggs than those fed on young green leaves (Table 11) but the difference was not quite significant at the 5 per cent. level. When the former food was given in the first two instars and the latter in the second two the number of eggs laid was between the above two values. Whenever mature leaves were given to the larvae in the second two instars of their life after feeding them on tender foods in the first two, their egg-laying capacity was depressed (effect significant at 1 per cent. level), but if this food was given only in the fourth instar the fecundity was not depressed so much.

Figure 3 shows the graphs of oviposition behaviour and longevity of female moths in different treatments.

Remarks

(1) Caterpillars used in the experiment emerged from the eggs over a period of 6 days from May 16 to 21, 1952, and on any one day the young larvae were distributed in one treatment. The incubation period of all the eggs was the same.

TABLE 11

AVERAGE NUMBER OF EGGS PER FEMALE FED ON DIFFERENT QUALITIES OF CABBAGE LEAVES AT 17°C

Mean based on 10 observations

Treatment No.	Food Given in Different Instars				Eggs per Month (S.D. ± 26.8)
	1st	2nd	3rd	4th	
1	A	A	A	A	274
2	A	A	A	B	160
3	A	A	B	B	221
4	B	B	B	B	201
5	B	B	B	C	163*
6	B	B	C	C	80
7	A	A	A	C	199
8	A	A	C	C	110
			General mean:		176
Min. significant difference (69 d.f.):			$P = 0.05$		76
			$P = 0.01$		100
			$P = 0.001$		130

* This value is based on seven observations only; all the remaining pupae failed to emerge. The S.D. of this mean is $S/\sqrt{7}$ or 32.0. The minimum significant differences for the comparison of this mean with other means in the table are: $P = 0.05$, 83; $P = 0.01$, 110; $P = 0.001$, 143. The analysis of variance showed treatments significant with $P < 0.001$.

(2) In treatment No. 5, 16 of the 23 female and 14 of the 20 male pupae died with characteristic symptoms not noticed in any other case. They became hard, looked as if calcified, and were dark brown in colour with dirty white spots on their bodies. No pathological organisms were found in them.

(*f*) *Experiment* 6: *Influence of Photoperiod and Quality of Cabbage Leaves on Fecundity*

Caterpillars were reared at two temperatures, 19 and 24°C, under 15-hr and 9-hr exposures to electric light in an incubator, on two types of cabbage leaves: A, grown in long day (15-hr photoperiod); B, grown in short day (9-hr photoperiod).

One type of cabbage was grown in earthen pots of 9-in. diameter, containing similar soils. Some of these were allowed to grow in ordinary daylight, about 9 hr in June-July 1952, and the rest were exposed to extra hours of electric light (40 W), 3 hr in the morning before sunrise and 3 hr

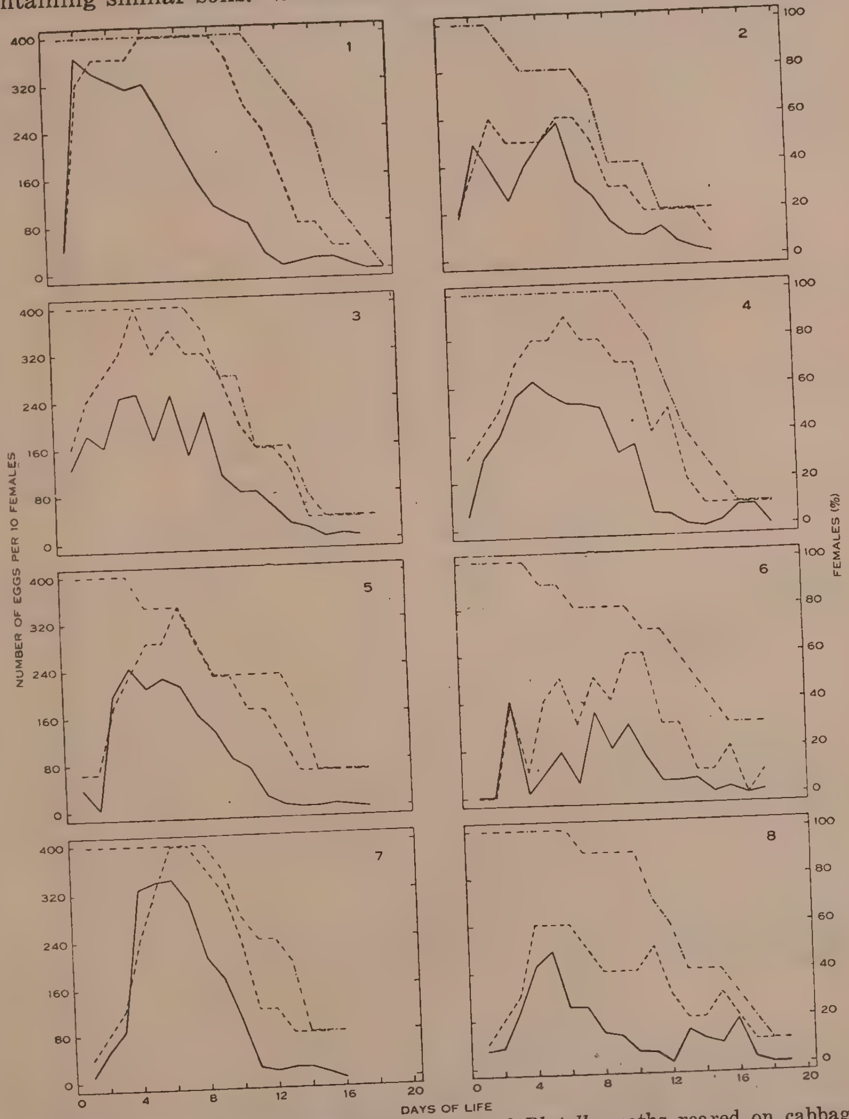

Fig. 3.—Fecundity and oviposition behaviour of *Plutella* moths reared on cabbage leaves of different ages (experiment 5). ——— Number of eggs; - - - - egg-laying females (% of original number); -.-.-. females surviving (% of original number). Graph numbers correspond to treatment numbers (Table 10).

in the evening after sunset, thus making a photoperiod of 15 hr. Plants were used for the experiment after 6 weeks' growth under these conditions.

Eggs were obtained from moths reared in experiment 4, and were incubated at 19 or 24°C alternately. The caterpillars (hatched within 6 hr) of a particular treatment were reared *en masse* in Fowler glass jars. To provide a required photoperiod in an incubator the jars were enclosed in light-proof metal tins; the same photo-conditions were maintained during the pupal stage. Almost all the caterpillars reared at 24°C died, so that half of the experiment had to be abandoned. Of the remaining treatments, all the females that reached adult stage were recorded every day. In each case two of the males were collected as pupae from the field.

TABLE 12

AVERAGE NUMBER OF EGGS PER FEMALE AT DIFFERENT LEVELS OF PHOTOPERIOD AND QUALITY OF CABBAGE LEAVES AT 19°C

Variable number of observations

(*A*) *Results*

Food Grown in	Rearing Photoperiod				Weighted Mean
	15 Hr		9 Hr		
	No. of Females	Eggs per Female	No. of Females	Eggs per Female	
Long day	17	212.2	10	216.2	214.1
Short day	15	149.7	10	178.3	164.0
Weighted mean		189.0		201.0	189.1

(*B*) *Summary of Effects*

Effect of	Eggs per Female
Food (long day — short day)	50.0
Photoperiod (9—15 hr)	16.0
Interaction (long day — short day) × (9—15 hr)	— 12.0
General mean	189.0
S.D.±	27.1
Min. significant difference (48 d.f.; $P = 0.05$): 55	

Analysis of variance: treatments non-significant but food taken alone nearly so ($P = 0.07$)

Caterpillars fed on cabbages grown in a long (15-hr) photoperiod laid more eggs than those fed on food grown in a 9-hr photoperiod each day (Table 12) but the difference was not quite significant at the 5 per cent. level. Figure 4 shows the graphs of oviposition behaviour and length of life of female moths in different treatments.

Remarks

At 24°C most of the insects died in the larval or the pupal stage. Since the leaves turned yellowish and looked unhealthy within a few hours, it appeared as if after growing the plants at low temperatures outside and then bringing them to the high temperature of the incubator, certain undesirable chemical changes occurred in them; it is interesting that those exposed to the same photoperiod in which they were grown remained in an apparently desirable condition for a longer period than the ones subjected to a different photoperiod in the incubator.

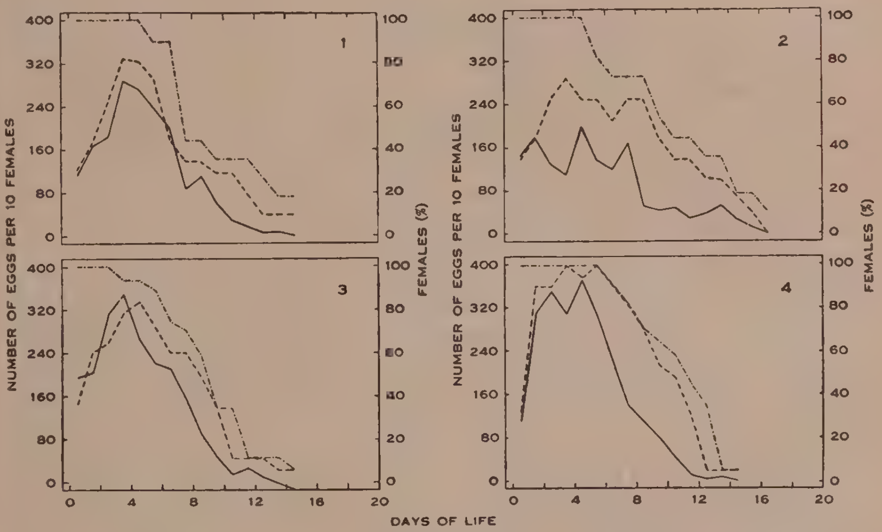

Fig. 4.—Fecundity and oviposition behaviour of *Plutella* moths at 19°C on different qualities of cabbage leaves in different photoperiods (experiment 6). ——— Number of eggs; - - - - egg-laying females (% of original number); -. -. -. females surviving (% of original number). Graphs 1 and 2, food grown in short day: 1, caterpillars reared in 9-hr photoperiod; 2, caterpillars reared in 15-hr photoperiod. Graphs 3 and 4, food grown in long day: 3, caterpillars reared in 9-hr photoperiod; 4, caterpillars reared in 15-hr photoperiod.

(*g*) *Experiment* 7: *Influence of Fertilizers given to Different Varieties of Cabbage on Speed of Development and Survival Rate of Larvae*

Caterpillars (hatched within 12 hr) were reared at 20°C, on two varieties of cabbage grown in a temperature-controlled room (75-80°F) and given different fertilizers. An attempt was also made to measure pot to pot and plant to plant differences. The factors were:

Variety.—Sugarloaf, Succession.

Fertilizer.—(1) Control. No fertilizer.
(2) Ammonium sulphate, 2 cwt/acre.
(3) Superphosphate, 4 cwt/acre.
(4) Potassium sulphate, 2 cwt/acre.
(5) Ammonium sulphate, 2 cwt/acre, + superphosphate, 4 cwt/acre.
(6) Ammonium sulphate, 2 cwt/acre, + potassium sulphate, 2 cwt/acre.
(7) Superphosphate, 4 cwt/acre, + potassium sulphate, 2 cwt/acre.
(8) Ammonium sulphate, 2 cwt/acre, + superphosphate, 4 cwt/acre, + potassium sulphate, 2 cwt/acre.

Pot.—Plants for each treatment were grown in two similar pots.

Plant.—There were two plants of equal size in each pot. Yates seeds of the above two varieties were used.

Plants were grown in earthen pots of 9-in. diameter filled with a homogeneous mixture of "Waite Institute soil" and washed beach sand in equal quantities. Five seeds were sown in each pot, nearly all of which germinated; when the plants had grown a little, two of them of the same height and equally healthy were kept. In all, there were 32 pots (arranged in eight rows of four each) which were placed on a wooden bench along the south double-glass wall of the temperature-controlled room. To give an equal chance of exposure to light to all plants, the pots were shifted in position within a row and from row to row twice a week. So far as possible, equal quantities of water were given to all plants. The plants were grown in February-March 1953 and the caterpillars were reared during April-May.

When the plants were 4 weeks old, they were given the appropriate fertilizers dissolved in distilled water in two doses separated by an interval of a fortnight. The quantities for each pot were at the rates per acre given above. The experiment was started 4 weeks after the second application of fertilizer. These three fertilizers were selected as all having the sulphate radical.

Eggs were obtained from moths reared in the laboratory. The eggs were incubated at different temperatures varying from 20 to 24°C, in the hope that they might hatch at more or less the same time. Hatching was spread over 2 days. At the end of each 12-hr period the larvae that had hatched since the last inspection were distributed at random but in equal numbers among all the treatments. Eventually 20 caterpillars were started on food from each of the 64 experimental plants. The 1280 larvae were reared in 640 tubes, two in each tube; their position in the incubator was fixed at random in batches of 10 tubes containing food from the same plant. Food was changed every other day after the first change, which was on the third day.

To measure the duration of larval and pupal life, observations were taken every 8 hr. The percentage survival of larvae under different treatments was converted to degrees (using Table XII of Fisher and Yates 1948) before the data were analysed. There was no significant difference between pots or within pots either in speed of development or in survival rate. In speed of development none of the effects was significantly different from the control.

TABLE 13

MEAN LENGTH OF LARVAL LIFE (DAYS) AND PERCENTAGE SURVIVAL (TRANSFORMED TO DEGREES) OF LARVA ON TWO VARIETIES OF CABBAGE GIVEN DIFFERENT FERTILIZERS

Based on 160 observations

Fertilizer	Average Length of Larval Life (days)		Percentage Survival*		Summary of Effects (survival)		
	Sugar-loaf	Succession	Sugar-loaf	Succession	Sugar-loaf	Succession	Mean
(1) **Control**	15.1	15.1	37.7	28.2			
(2) Ammonium sulphate	14.9	15.2	32.4	28.7	—1.5	4.4	1.4
(3) Superphospate	16.4	16.2	29.8	22.1	—6.4*	—3.9	—5.2**
(4) Potassium sulphate	14.9	15.0	34.4	28.8	—1.2	3.4	1.1
(5) **Ammonium sulphate** + superphosphate	15.0	15.6	27.1	27.3	1.9	—0.1	0.9
(6) **Ammonium sulphate** + potassium sulphate	15.0	15.2	32.8	36.1	2.5	1.4	1.9
(7) **Superphosphate** + potassium sulphate	15.4	15.5	25.8	26.3	0.2	—0.1	0.1
(8) **Ammonium sulphate + superphosphate** + potassium sulphate	14.3	14.6	29.2	29.5			
					31.1	28.2	29.7
Mean					1.2$^{(a)}$		0.85$^{(c)}$
S.D.±					2.4$^{(b)}$		1.7$^{(c)}$
S.D.=							

Min. significant difference (48 d.f.):

	(a)	(b)	(c)
$P = 0.05$	3.5	4.9	3.5
$P = 0.01$	4.6	6.6	4.6
$P = 0.001$	6.1	8.6	6.1

* Transformed to degrees, using Table XII of Fisher and Yates (1948).

A higher death-rate was observed among caterpillars fed on cabbage given phosphate fertilizer (the difference from the control was significant at the 1 per cent. level), but the death-rate among those fed on the plants given nitrogen and potash was no different from the control (Table 13). Similarly speed of development on the phosphate-treated plants was slower than on the others, but the difference was not significant.

(*h*) *Experiment* 8: *Influence of Temperature and Photoperiod on Fecundity*

Caterpillars were reared at two temperatures, 15 and 20°C, under 9-hr and 15-hr exposures to electric light (40 W) in incubators on two types of food: A, cabbages grown in a long day (15 hr of light); B, cabbages grown in a short day (9 hr of light).

The nursery plants were procured from a local shop and grown in earthenware pots under two photoperiods, in the same manner as described in experiment 6, during July-August 1952.

Eggs from moths reared in the laboratory were incubated at 25°C. For rearing, caterpillars were started in individual tubes. Food was changed and tubes were cleaned every other day. Almost all the caterpillars died sooner or later. Comparatively few caterpillars mined into leaves when food was provided within 8 hr of hatching. The larvae which survived during their earlier instars died from disease after some days. The following pathogenic organisms were identified from the dead larvae:

(1) Fungus.—A strain of *Aspergillus flavus* Link (fam. Aspergillaceae).

(2) Bacteria.—(i) Red. Small grain, negative rod, coagulates milk, does not produce gas from glucose, rapidly liquefies nutrient gelatin with formation of sediment, agar slope cultures bright red at 25°C, white and slightly less growth at 35°C:

Serratia sp., probably closest to *S. marcescens,* atypical because of growth at 35°C.

(ii) White. Small grain, negative rod, non-motile at 35°C, motile at 25°C, growth greater at 25°C, slowly ferments lactose with production of acid, gives acid and gas from glucose, grows on McConkey's agar, is positive to methyl red and negative to Voges-Proskauer, utilizes citrate as sole source of carbon, coagulates litmus milk:

Aerobactor aerogens, atypical in that it is much slower to ferment lactose than are typical cultures of this organism.

The above microorganisms were most probably the indirect cause of death in the caterpillars. It is possible that the food was unfavourable and that this reduced the vigour of the caterpillars, making them more susceptible to disease. In the incubators the pieces of leaves remained quite turgid, green in colour, and apparently quite normal. The seedling plants which were bought as such might have been of some resistant strain or of a variety out of season.

(*i*) *Experiment* 9: *Effect of Quality of Food on Sterility in Males*

In experiment 5 it was seen that the quality of food eaten had a profound influence on the fecundity of female moths. To investigate whether males would be similarly influenced by food two sets of caterpillars were reared in January 1953 on white leaves from the heart and maturer green leaves of cabbage. On emergence the male and female moths from these were treated in the following manner:

(1) Each of 10 males from white food were placed in a cage with one female from white food. As soon as the female started laying eggs (which showed that it had been fertilized) it was taken out and replaced with a new unmated female. This was repeated while the male remained alive. All the 10 males mated with at least one female, three with two females each, and one even with three females during its lifetime.

(2) Fifty females were kept without males, and none laid any eggs.

(3) Of 20 females from white leaves, selected at random, half were kept with 10 males (one each) from white food and the others with 10 males from green leaves. In the former set all 10 females were fertilized, whereas in the latter only six laid eggs. These results suggested that poor quality of food might cause sterility in males. There were not enough observations for the significance of the results to be tested statistically.

IV. DISCUSSION

(*a*) *Speed of Development*

(i) *Influence of Temperature and Photoperiod.*—The results in Tables 6*A*, 6*B*, and 9 show that caterpillars kept at a constant temperature but exposed to 9 hr of light each day took longer to complete their larval development than those kept at the same temperature but exposed to 15 hr of light each day. When the temperature was varied as well it was found that the decrease in speed of development with decreasing temperature was greater for larvae exposed to 9 hr than for those exposed to 15 hr of light daily. The converse was also true. This means that the same photoperiod had a different influence at different temperatures. In other words the greatest reduction in speed of development occurred when the larvae were exposed to a combination of short photoperiod and low temperature.

Similar interactions between temperature and photoperiod are known to occur with certain other species which enter diapause in response to similar stimuli (Dickson 1949). The analogous response by *P. maculipennis* suggests that the condition of larvae reared at low temperature and short photoperiod might be compared with the beginnings of a faint or incipient diapause. It was indeed noticed that when larvae were reared in cages exposed to natural temperatures and photoperiods a proportion of them would, during winter, remain as larvae for almost twice the time usually taken. This never happened when larvae were reared in the same cages during summer.

(ii) *Influence of Quality of Food.*—The most striking responses to variations in the quality of food were observed when old senescent leaves were compared with young green leaves and white leaves from the heart of the cabbage (Tables 1, 2, 3, 4, and 5). With senescent leaves the larvae grew scarcely at all, and all died before reaching the third instar.

Larvae which were reared on white leaves from the heart of the cabbage or on the young quick-growing green leaves developed more quickly than those which were reared on leaves which were green and healthy but mature.

When the larvae were reared on leaves which were in a particular stage of development (either young white or young green), but grown in various photoperiods or in soils receiving various levels of fertilizers, there was no significant difference in the speed of development of larvae reared in any one photoperiod; but when the photoperiod experienced by the larvae was also varied the following interaction was found to be just significant at the 5 per cent. level. When plants which had been exposed to 9 hr of light each day were used as food there was an indication that the larvae would develop more slowly if they were exposed to 9 hr of light each day than if exposed to 15 hr. On the other hand when plants which had been exposed to 15 hr of light each day during growth were used as food there was no difference in the speed of development of larvae exposed to 9 and 15 hr of light each day. It was also noticed that, in an experiment done during the summer, the caterpillars exposed to 9 hr of light daily developed rather slowly (Table 9). Taken together these results suggest that short photoperiod, apart from having a direct influence on the speed of development of the larvae, also had a similar effect on them indirectly through their food. However, the experiments would need to be repeated with larger numbers to establish this point convincingly.

The results in Table 1 indicate a rather unexpected interaction between temperature and food. Larvae reared on mature leaves spent a longer time in the larval and pupal stages than those reared on the other sorts of food, at both 18 and 25°C, but the increase in the time required for development was relatively greater at 18°C than at 25°C. If the slowness of development was due to the maturity of the leaves and if the processes of maturation went on more quickly at 25°C than at 18°C, then one might have expected the opposite result. In nature the mature leaves would more often be present during the hotter season. Thus a possible explanation for this interaction might be that *P. maculipennis* is adapted to make better use of mature leaves at higher temperature. A possible mechanism might be that the higher temperature, by increasing the vigour of muscular activity, may increase the larva's ability to ingest the coarser food more than it increases its need for food.

(iii) *Factors other than Temperature, Photoperiod, and Food.*—In experiment 3, caterpillars hatched on October 26 and 28 developed more quickly than those hatched on October 24 and 25. Since there was no difference in the food this could not have been the cause. Temperature and light were similar in all corresponding treatments.

To obtain the larvae for experiment 3, eggs were incubated at 20°C at night and 24°C during the day. The eggs which hatched on October 24 were not exposed to artificial light; those hatched on October 25 got a constant exposure to electric light during the last 24 hr of their embryonic life. However, the eggs which hatched on October 26 and 28 were constantly exposed to light for either the whole or most of their embryonic life. It has been noticed that normally the caterpillars emerged from the eggs during the day and very few or none at all during the night or in complete darkness, which suggests that light may act as a stimulus at least to the fully developed embryo. One explanation for the results obtained in experiment 3 might be that the eggs laid by moths of overwintering generations are in such a condition that if they are incubated in continuous light (or long photoperiod) the larvae develop more quickly than those which hatch from eggs incubated in a short photoperiod. In order to test this hypothesis another experiment (4) was laid out, in which eggs were incubated and caterpillars were reared in different photoperiods at 17°C. As may be seen from Table 9, the speed of development of the caterpillars incubated in 9 hr of light each day was no different from those incubated in 15 hr. However, this was at 17°C, and had the experiment (4) been conducted at 20-24°C different light exposures during incubation might have influenced the speed with which the larvae subsequently developed. This still remains to be tested by further experimentation.

In experiment 3 the majority of the moths collected from the field died after laying eggs for 2-3 days; thus most of the eggs which hatched on October 24 and 25 were from short-lived females, whereas the remainder came from females which lived longer and perhaps had greater vitality. There may have been a difference in the physiological condition of the moths which might have been impressed on their eggs, resulting in different speeds of development of their progeny. Moreover, some of the moths were collected from cabbages and some from swedes but they were not kept separately in the laboratory. If by chance most of the eggs which hatched on October 24 and 25 had been laid by moths from swedes then there is the possibility that the cabbage is less suitable as food for progeny of insects which fed on swedes than for those that fed on cabbages in the field. There is no evidence that this is so with *Plutella*, but for certain other species it is known that the progeny tend to prefer the food eaten by their mothers, e.g. the sawfly *Pontania salicis* (Harrison 1927), the icheneumonid *Nemeritis canescens* (Thorpe and Jones 1937), and the stick insect *Carausius morosus* (Sladden and Hewer 1938).

(iv) *Difference between Sexes.*—Irrespective of temperature and quality of food, females developed more slowly than males and since they also had more dry matter and a higher liveweight in the pupal stage, it appears that this extra time is utilized for eating more food. If the influence of temperature and food on the weight of pupae and their water content is considered in relation to the differences between the sexes in pupal weight and water content, it appears that the female may fulfil its requirements better from a good quality food at moderately low temperatures, whereas a male may be better able to develop on poorer food at higher temperatures. The effects of quality of food on various characteristics of male and female were highly significant (experiment 1, Tables 1, 2, 4, and 5).

(b) *Fecundity*

(i) *Influence of Temperature, Food, and Photoperiod on the Number of Eggs Laid.*—The number of eggs laid by a moth during its lifetime was influenced by the temperature at which the caterpillar was reared and the temperature at which the moth was kept. Insects which were kept throughout their larval and adult lives at 18°C laid more eggs than those which were kept at 25°C (Tables 6*A* and 6*B*). Larvae reared at 18°C gave rise to heavier adults than those reared at 25°C. The adults also lived for a shorter time at 25°C. However, it is considered that the difference in fecundity is chiefly due to differences in weight. On the other hand the insects which were reared as larvae at 18°C and kept at 21°C as adults laid fewer eggs than the controls, which were kept throughout their lives at 18°C (Table 7). In this case there was little difference in the weights of the moths, and the difference in fecundity must have been associated with the shorter life of the moths which were brought as adults to the higher temperature (Table 7).

Moths reared from caterpillars exposed to 15 hr of light each day laid on an average 32 more eggs than those reared from caterpillars exposed to 9 hr (Tables 6*A* and 6*B*). In this experiment the larvae developed more slowly at the shorter photoperiod and, by analogy with temperature, one might have expected them to be heavier and to have laid more eggs than those which developed more quickly. But the converse happened; and this may be taken as an indication that temperature and photoperiod influenced speed of development and fecundity in different ways. It is possible that the influence of photoperiod on fecundity in *Plutella* is analogous to its influence on diapause in other species.

The influence of the quality of food eaten by the larvae on the number of eggs laid by the moths was studied in two ways: (1) larvae were reared on leaves taken from different parts of the cabbage and consequently at different stages of development; (2) larvae were reared on leaves selected for uniformity in stage of development, but grown under different photoperiods.

In experiment 5, moths which were fed on white leaves from the hearts of cabbage plants during their larval life produced the highest number of eggs, the average being 274 per female (Table 11); on the outer quick-growing young green leaves the average was 201 eggs per moth. The difference between these two types of food was not quite significant at the 5 per cent. level.

When white leaves were given to the first two instars and young green leaves in the second two, the number of eggs per moth was 221, which is between the values for these two foods given separately but nearer to that obtained when young green leaves were given throughout the larval life. This shows that the effect of food eaten in the last two larval instars is dominant over that eaten in the first two instars.

In those cases where it was desired to use the mature leaves it was necessary to rear the larvae for the first two instars on white or young green leaves and then change to mature leaves for the later instars; this resulted in fewer eggs from the adults. The differences were significant at the 0.1 per cent. level. Slightly more eggs were laid on the combination of white followed by mature leaves.

The favourable effect of good quality food appears to be cumulative when fed during a part of the larval life. As may be expected perhaps, the effect of food eaten during the last larval instar is dominant over that taken in the first two instars. When the larvae were given the better quality food during the first three instars the moths laid more eggs than those which had received the good food for only two instars (Table 11, treatments 2, 5, and 7). However, in one treatment in which caterpillars after feeding on white leaves in the first three instars were given young green leaves in the fourth (Table 11, treatment 2) the egg-laying capacity was not as high as would have been expected in view of the desirable effect of white leaves. This may have been accidental or some unnoticed factor might have had an influence.

In general the moths which were reared on a good quality food and which laid a high total number of eggs showed regular curves of oviposition, whereas those reared on an inferior food showed great variation in the number of eggs laid on different days of their lives (Fig. 3).

In experiment 2, plants growing during summer were exposed to 9 and 15 hr of light daily, and in experiment 6, plants growing during winter were exposed to the same photoperiods. In each case slightly more eggs were laid by moths which had been reared as larvae on the plants exposed to the longer photoperiod (Tables 6*A*, 6*B*, 12*A*, and 12*B*); but in neither case was the difference significant. The fact that the difference was in the same direction in each experiment suggests that it might be possible to demonstrate a small effect by using more replicates of various treatments. The curves of number of eggs laid by moths on different days of their lives also show some indication in the same direction (Figs. 2 and 4).

It was noticed during these experiments that the food kept its condition better when exposed to the same photoperiod as that in which it had been grown. In experiment 5, caterpillars fed on food grown in 9 hr of light each day laid more eggs when reared under a 9-hr photoperiod than under a 15-hr (in a 15-hr photoperiod the leaves in the incubator became yellow earlier than in a 9-hr photoperiod), with a difference of 28 eggs per female; moreover, moths laid in a very irregular manner (Fig. 4, curve 2). However, the interaction was again not quite significant.

(ii) *Relation between Longevity and Fecundity of Moths.*—It was observed in these experiments that generally the female moths which lived longer laid the higher number of eggs. As a rule a greater number of such long-lived moths was produced on white or young green leaves of cabbage than on mature green leaves. The females living for a longer period usually laid eggs regularly, whereas the short-lived moths reared on poor quality food laid eggs in a very irregular manner (Fig. 3, curves 6 and 8). When the total number of eggs laid by 10 females reared on poor food was plotted against time, the curves showed that laying fluctuated sharply from day to day, whereas those females which were reared on better quality food did not fluctuate so much in their laying and the graphs showed smoother curves. Moreover, a greater proportion of living females reared on good quality food laid eggs every day than those reared on a poorer diet (Fig. 3, curves 1, 5, and 7).

(iii) *Influence of Food on Sterility in Males.*—Since a female does not lay eggs without fertilization and quite often mates more than once during its life, it was thought desirable to study the influence of quality of food on the mating capacity of the males. In the only experiment done with males there was an indication that the males reared as larvae on mature leaves tended to be sterile while those reared on young white or young green leaves were fertile; but the experiment contained too few replicates to demonstrate the significance of the difference (experiment 8). It was also found that some of the fertile males were capable of fertilizing two or even three females during their lifetime.

(iv) *Body Weight in Relation to Production of Eggs and Silk.*—Usually the caterpillars which were heavier spun more silk and developed into moths that laid more eggs. Caterpillars tended to grow larger and to develop into heavier pupae when reared at a lower temperature (compare 18°C with 25°C, Table 9), and on good food (compare white or young green leaves with old leaves, Table 1), but photoperiod, though it influenced the speed of development, seemed to make no difference to the weight of the larvae.

Males were usually smaller and lighter than females and spun less silk; and the ratio of dry matter to water was consistently higher for females than for males. The females also tended to develop more slowly than the males. It is considered that these differences between the sexes may explain the significant interactions between food and sex recorded in Tables 1, 2, 4, and 5. It may be that the male is better able to develop on poorer food and at higher temperatures than the female.

With females, when the differences in body weight were due to differences in temperature the ratio of dry matter to water remained constant, but when differences in the weight of the pupa were due to differences in the food of the larva there was a tendency for the lighter pupae to contain relatively less dry matter than the heavy ones.

(c) *Survival Rate among Larvae*

(i) *Quality of Food.*—On senescent leaves of cabbage, caterpillars did not survive even when this food was given after feeding them on white or young green leaves in the first two instars (experiments 1 and 5). Since during senescence there is very little photosynthesis going on in the leaves, the amount of food materials present would be very low. Such a food may be inadequate as a diet. Moreover, the proteins present in the tissues of a leaf are broken down and are utilized as a source of energy, with the result that the percentage of water in the cell sap is increased. Perhaps the larvae did not get full nourishment when fed on this food; or perhaps during the breakdown process some injurious by-products were produced in the sap which caused death.

Newly hatched caterpillars failed to eat mature leaves (probably the cuticle is too hard), but when they were fed on tender young leaves in the first instar and mature leaves in the second instar they remained weak, development was slow, and large numbers died during larval life. If this food was given only in the third and fourth instars, the speed of development was not so slow and the death-rate was also reduced; but those which pupated weighed less and contained relatively more water than the pupae which were fed on tender young leaves throughout their larval period (experiment 1, Table 5).

White and young green leaves from the same cabbage plant given throughout larval life were most suitable for development and on these the survival rate was much higher than with the other two foods. The moths reared on these foods lived for a long time and a high percentage of the females living laid eggs every day (Fig. 3). When caterpillars were fed on leaves which looked apparently normal but were unsuitable in some other way, their health was very much affected and they were more susceptible to bacterial and fungal disease, with the result that a great proportion of them died (experiment 8).

In the field the availability of young and tender leaves of cabbage to the newly hatched caterpillars is very important for their survival. Concentration of too many larvae on a small surface may also result in spoiling the fresh leaf. High death-rates, therefore, may occur owing to a change in the quality of food caused by the feeding of the caterpillars themselves. During the first two instars the caterpillars, because of their small size, cannot go very far in search of better food, so they are especially vulnerable in this early stage of their development. The larger larvae are more motile.

A mature crop of cabbage is therefore of no use to *Plutella* unless enough tender leaves are present for newly hatched caterpillars to mine in. It has been noticed in the field that the population tends to increase most in a field of young cabbages. In young plants the insects tend to concentrate towards the centre, with the result that if they are numerous, the heart may not be formed. However, if the heart has already formed at the time when most of the eggs are being laid, it becomes bigger from within, forming a covering of mature leaves on the top, so that the plant does not suffer a severe loss from insect attack although the caterpillars go on feeding on the outer layers of the heart. In such advanced cases, dew forms on the centre of the cabbage; this moist condition is not suitable for the spinning and attachment of cocoons. The majority of caterpillars are seen feeding in the heart for the first three instars and in the fourth they move out to feed on maturer leaves and pupate there. It is in the centre of the plants that the larval parasite *Horogenes* (*Angitia*) searches for caterpillars, whereas the pupal parasite *Diadromus* is more commonly observed in between the large mature leaves. Ullyett (1936, 1943) studied the host-parasite relationship of *Plutella* and *Horogenes* (*Angitia*), and found that in the field superparasitism was related to the number of host larvae per plant, and in this connexion he pointed out the importance of the growth factor in cabbage plants.

This would mean that when the cabbage plants are young and the weather has already warmed up there are greater chances of their being damaged by the pest, firstly, because the moths will lay eggs on tender leaves, and secondly, because the parasites may be less active (Ullyett 1947). With increase in surface area of the crop, however, there will be a tendency towards moderation in density of the host insect. A practical use of this observation can be made by sowing the spring cabbages early so that their hearts may be formed before the expected time of appearance of the pest.

(ii) *Resistance in Plants.*—The survival rate of caterpillars fed on plants given nitrogenous and potassium fertilizers was not different from that of those on the controls, but the addition of phosphate caused a higher mortality; the difference was significant at the 0.1 per cent. level (experiment 7, Table 13). The leaves of the plants receiving additional phosphate seemed to be stouter than the others.

More caterpillars reached the adult stage on the variety Sugarloaf than on Succession, and the decreased survival rate associated with superphosphate was greater for Succession than for Sugarloaf. However, neither the difference between varieties nor the interaction with phosphate was quite large enough to be significant.

(iii) *Body Form and Survival Rate.*—The insects reared on poorer quality food (such as the mature leaves of cabbage) were small. Many of them died prematurely and some showed deformities in wings and antennae. The wings were stumpy and the antennae dropped. When the larvae were reared at high temperatures, again many moths were found with non-erectile antennae but this cause should be differentiated from that of quality of food. In this case the insects were also unable to balance their bodies properly.

Caterpillars showed a tedency to stop feeding and moult if the food started to decay and, depending upon the quantity of such food eaten, they either died in the pupal stage or emerged into abnormal moths with or without the above-mentioned deformities.

Females from any of the above groups were found to be most variable in length of life and egg-laying. Curves showing the number of eggs laid on different days of life showed great fluctuations, whereas curves of groups of females fed on good food (white or young green) under favourable conditions of photoperiod and temperature were much smoother (Fig. 3).

A small percentage of the larvae, especially in the winter experiments, lingered behind the others so that sometimes they took even double the normal time to develop. Usually with these individuals the duration of the prepupal and pupal stages was also longer. These "slow-growing" caterpillars were usually sluggish, did not spin normal cocoons, and included a large proportion of the females which failed to lay eggs. On dissection they were usually found to be full of eggs. The cause of their failure to lay eggs could not be found; there is little doubt that they got a fertile male.

(*d*) *General*

(i) *Balance of Nutrients Required by Insects.*—From the above experiments and work done on other insects it would appear that the quality of food eaten has a direct influence on the speed of development, survival rate, general activity, and fecundity of insects. The difference in quality may be as found in different host species for a polyphagous insect or due to difference in the physiological stage of development of the host in a monophagous insect. Depending upon the quality of food eaten in the pre-imaginal stages, the insects may attain different body weights. Apart from the influence of food the insects that develop slowly owing to a low temperature of rearing may also become heavy, presumably by eating more food. Slow speed of development due to the influence of photoperiod may also be associated with an increase in body weight. In other words, physical factors of the environment like temperature and photoperiod influence the insects directly or through the host plants in such a way that the quality of food materials stored in their bodies may be affected. If so, it is logical to think that in turn the metabolic activity would also be governed by the same factors.

The physiological condition of the plant as influenced by age, type of soil, and other factors of the environment forms, therefore, a very important basis for the study of its resistance to insect attack. It may be true that a plant which looks weak in health may be easily attacked by insect pests but the insects can live on it only if it provides adequate nourishment. On the other hand a plant may look quite healthy but may contain an excess of some nutrients which may impart immunity to it against the attack of insects (perhaps by changing the water ratio). The high death-rate among *Plutella* caterpillars feeding on cabbages getting an excess of phosphate fertilizer may be a case in point.

It appears that for normal metabolism an insect requires a certain optimum quality of food containing the right proportion of nutrients. Since growing plants are subject to the influence of external environment, such an optimum quality may or may not be available throughout the year. With change in environment (especially physical) certain corresponding changes in the constituents of plants would be expected. Some of the nutrients in the plants may be present but not in sufficient quantity relative to the others (as found in different species or varieties of a host plant) or some may be present in amounts that are too large relative to the others; in neither case would there be a proper balance of the nutrients required for normal activity and reproduction; and certain abnormalities may appear in insects feeding on such plants. Deficiencies in the food may result in deformed or unhealthy adults. In extreme cases very few larvae may survive to become adults. If no vital nutritive factor is deficient in the food but some of the constituents are present in excessive proportions the insect feeding on it may end by storing an excess of some nutrients (e.g. increased fat-body in diapausing insects), thus exhibiting a regular phenomenon governed by the season of the year. This process may be associated with slow speed of development, and the normal metabolism may be upset as a result of the excessive material stored in the body. This general conclusion about the balance of nutrients required by insects for normal activity may be a useful hypothesis on which to base future work.

(ii) *Diapause in Insects.*—The phenomenon of diapause is quite well known among insects. Shelford defined it in 1929 and kept it quite distinct from quiescence. Andrewartha (1952) pointed out that obligatory diapause is often found in insects with univoltine life cycles which show a seasonal rhythm. Facultative diapause is more usual in multivoltine insects. In species in which the diapause is facultative there is usually a causal relationship between the seasonal variation in certain components of environment and the incidence of diapause (Kogure 1933; Dickson 1949). In both cases certain symptoms are common, for example, slow speed of development prior to the onset of diapause especially towards the later stages of larval development, excessive storage of food materials in the body, or reduction in the water content of the body. Andrewartha's theory, which attributes diapause to the accumulation of intractible stores of food materials in the tissues of the diapausing individual, suggests a relationship between the breakdown processes and the activity of neuro-secretory cells that secrete the growth-promoting hormones necessary for the resumption of post-diapause development.

Diapause is not known to occur in *Plutella*; this insect becomes inactive when the temperature is too low but at optimum temperatures can be bred throughout the year. Nevertheless it responds to various factors of the environment such as temperature, quality of food, and photoperiod in the same way, but to a lesser degree, as certain other species in which diapause is known to occur. The quality of food eaten influences the contents of the body. The insects that fed on food containing a high percentage of water (mature leaves of cabbage) had a greater proportion of water in their bodies than those which fed on food containing more digestible dry matter (white or young green leaves). This influence of food affected both total body weight and ratio of dry matter to water in the body. These symptoms although milder in degree are, in general, similar to the ones found in diapausing insects. In *Plutella* also towards late autumn a small proportion of caterpillars showed unusually slow speed of development when they near pupation. It would seem that a seasonal rhythm of activity is exhibited by this insect, although it is not so pronounced as that found in those univoltine or multivoltine insects which enter diapause.

(iii) *Rhythm in Seasonal Activity of Insects.*—The influence of the physical factors of the environment directly or through food on the speed of development in insects shows how their activity may be synchronized with various seasons of the year. This synchronization is very pronounced in insect species in which diapause occurs. The seasonal rhythm is strongly evident in diapausing insects; in non-diapausing insects the rhythm may be only faintly evident but it is essentially of the same kind. This should not be surprising since the stimuli arising from the same components of environment (weather, food, etc.) are likely to be of a similar nature for diapausing and non-diapausing insects. In other words, life cycles tend to be influenced by the environments in which the animals are living. In some species the adaptation takes the form of a rhythm in the sequence of dormancy, activity, etc. and is dependent upon diapause, but in others the adaptation may consist in the timing of the life cycle, i.e. in the rate of development and the time taken to come to maturity, etc. Behaviour and development in these species may be nicely adjusted to the seasons. Of course any variants which are not so adjusted do not stand much chance of surviving.

Since Darwin's day there has been a tendency to consider the process of evolution and natural selection as resulting in species becoming attuned to their environment in such a way that they are beautifully fitted to live in the places in which they are found. However, it is quite commonly seen that populations fluctuate in numbers between wide extremes. In experiments conducted with *Plutella*, although it is apparent that its behaviour and activity in various seasons are set on certain patterns as influenced by various factors of the environment and show a beautiful picture of adaptation, in the field such wild fluctuations in population may occur (see Ullyett 1947) as would be difficult to explain in the presence of moderating factors operating promptly. The recurrent heavy reductions in number which many species suffer suggest that the adaptations are not so efficient as may at first sight appear, but are merely the best that can be achieved through selection when the violent fluctuations in the environment are taken into consideration.

V. Acknowledgments

I am grateful to Dr. H. G. Andrewartha for his kind guidance and supervision of this work. To Mrs. I. Mathison I am indebted for her advice and for checking the calculations. Mrs. B. Passey very kindly identified the species of bacteria and Dr. J. H. Warcup the moulds. The work was carried out during tenure of a Research Fellowship awarded by the Commonwealth Government under the Colombo Plan.

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PATTERNS OF SPERMATOGENESIS IN GRASSHOPPERS

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(*Manuscript received December* 2, 1954)

Summary

The number of generations of secondary spermatogonia ranges from 4 to 9 in 66 species of grasshoppers studied and the number of sperms per sperm bundle from 64 to 2048.

I. INTRODUCTION

In the course of work on cytological polymorphism in natural populations of a number of species of grasshoppers some observations were made on what we may call the "pattern of spermatogenesis". The data seem worth publishing since very little has been recorded concerning cell lineage and histological patterns in the insect testis.

In all grasshoppers, as in other orthopteroid insects, the testis consists of paired finger-shaped follicles, connected to vasa deferentia at the lower end. Laird (1943) studied the gross anatomy of the testis in about 100 species of Acrididae and described two main kinds of testes: the "radiating" type, in which numerous relatively short follicles enter the vasa deferentia along a considerable part of their length, and the "fountain" type, in which a much smaller number of slender, elongated follicles enter the vasa in a cluster at the anterior end. However, all intermediates between these two extreme types exist.

Laird found that the radiating type existed in the subfamilies Pyrgomorphinae, Pamphaginae (together constituting the section Chasmosacci of the Acrididae), and also in the Romaleinae, Ommexechinae, and some of the Cyrtacanthacridinae (all of which belong to the section Cryptosacci). Many Cyrtacanthacridinae possessed an "intermediate" type of testis, and a few had the fountain type. The latter is characteristic of the subfamilies Oedipodinae and Acridinae, in which the radiating type does not occur.

Laird did not deal with the comparative histology of the testis. In general, it can be said that near the tip of each follicle there is a group of primordial spermatogonia and interstitial cells arranged around a single apical cell which may have a specialized nutritive function (Carson 1945). The primordial spermatogonia divide to form secondary spermatogonia which become surrounded by interstitial cells. Each group of secondary spermatogonia with its sheath of interstitial cells is known as a cyst. The cysts gradually pass down the follicles and eventually become the sperm bundles which are passed out into the vas deferens. Successive

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divisions of the secondary spermatogonia are always synchronous within the cysts, so that the number of cells within a cyst is always a power of two. After a certain number of generations of secondary spermatogonia the cells become converted into primary spermatocytes and enter on the meiotic divisions. Since there are two of these, the number of sperms in a bundle is necessarily four times that of the primary spermatocytes in a cyst.

II. OBSERVATIONS

The number of generations of secondary spermatogonia ranges from 4 to 9 (and hence the number of primary spermatocytes per cyst from 16 to 512) in the species of Acridoidea studied (Table 1). Within the individual species, however, this number is with few exceptions rigidly fixed. The data of Table 1 are derived from counts of primary spermatocytes in serial sections cut at approximately 25 μ. The values in the first and third columns are calculated from those in the second column. Included in the table are 66 species, 45 being North American, 20 Australian, and one (*Bryodema tuberculatum*) European.

It will be seen that the grasshoppers of the family Eumastacidae (or at any rate those belonging to the subfamily Morabinae, since members of other eumastacid subfamilies were not available for study) are characterized by a very high number of spermatocytes per cyst. The histology of the testis is somewhat different in these Morabinae from that seen in the Acrididae. In the latter a transverse section of a follicle shows several cysts, each of which occupies a sector of the follicle (like slices of pie). In the Morabinae, on the other hand, a transverse section of a follicle only cuts through a single cyst, the cysts being shaped like short sections of a cone. The cells within these cysts are small and crowded, with relatively little cytoplasm. The testis of the Morabinae is a rather extreme example of the radiating type.

Within the Acrididae the members of the subfamily Pyrgomorphinae seem to be characterized by seven to eight generations of secondary spermatogonia. The general arrangement of the cysts is the same as in the other Acrididae, but the cells are small and crowded. Unfortunately material of the subfamily Pamphaginae (the other main division of the Chasmosacci) was not available for study.

By far the majority of the Cryptosacci show six generations of secondary spermatogonia, i.e. there are 64 primary spermatocytes per cyst. But there are a number of species which normally have seven such generations, and several aberrant members of the North American tribe Melanoplini (*Campylacantha, Hypochlora, Dendrotettix,* and *Paratylotropidia*) only have five. The Texas species *Phaulotettix compressus* Scudder is unique among the species studied in having only four generations, i.e. only 16 primary spermatocytes per cyst. Members of the large genus *Melanoplus*, however, show seven generations of spermatogonia (judging from the four species examined). Among the relatively few

TABLE 1

NUMBER OF DIVISIONS IN GRASSHOPPER SPERMATOGENESIS

Species	No. of Generations of Secondary Spermatogonia	Primary Spermatocytes per Cyst	Sperms per Bundle
EUMASTACIDAE			
Moraba amiculi Sjöstedt, *collina* Rehn, and *scurra* Rehn*	9	512	2048
Keyacris marcida Rehn*	9	512	2048
ACRIDIDAE			
Section Chasmosacci			
Subfamily Pyrgomorphinae			
Atractomorpha c. crenaticeps (Blanchard)*	8	256	1024
Monistria ligata I. Bolivar*	7	128	512
Psednura musgravei Rehn*	8	256	1024
Section Cryptosacci			
Subfamily Cyrtacanthacridinae			
Goniaea australasiae (Leach)*	6	64	256
Cratilopus (?) sp.*	6	64	256
Perunga ochracea Sjöstedt*	6	64	256
Percassa rugifrons (Stål)*	6	64	256
Epallia sp.*	6	64	256
Zabrala sp.*	6	64	256
Macrolopholia sp.*	6	64	256
Perelytrana sp.*	6	64	256
Rusurplia sp.*	6	64	256
Hesperotettix viridis nevadensis Morse	6	64	256
Campylacantha olivacea vivax (Scudder)	5	32	128
Chloroplus cactocaetes Hebard	6	64	256
Hypochlora alba (Dodge)	5	32	128
Phaulotettix compressus Scudder	4	16	64
Paratylotropidia brunneri Scudder,	5	32	128
Dendrotettix zimmermanni (Saussure) *morsei* Rehn & Rehn, and *beutenmulleri* Morse	5	32	128
Melanoplus snowii Scudder, *femur-rubrum* (De Geer), *packardii* Scudder, and *gladstoni* Scudder	7	128	512
Phoetaliotes nebrascensis (Thomas)	7	128	512
Subfamily Oedipodinae			
Austroicetes pusilla (Walker)*	6	64	256
Aiolopus tamulus (Fab.)*	6	64	256
Pycnostictus seriatus Saussure*	6	64	256
Spharagemon collare (Scudder)	6	64	256
Dissosteira spurcata Saussure	6	64	256
Mestobregma plattei (Thomas) (subsp.?)	6	64	256

TABLE 1 (*Continued*)

Species	No. of Generations of Secondary Spermatogonia	Primary Spermatocytes per Cyst	Sperms per Bundle
Mestobregma terricolor Rehn	7	128	512
Trimerotropis acta Hebard, *bilobata* Rehn & Hebard, *latifasciata* Scudder, *melanoptera* McNeill, *pistrinaria* Saussure, *cincta* (Thomas), *fontana* (Thomas), *saxatilis* McNeill, *schaefferi* Candell, *suffusa* Scudder	6	64	256
Trimerotropis sparsa (Thomas), *gracilis* (Thomas), *thalassica* Bruner, *cyaneipennis* Bruner, *caeruleipennis* Bruner	7	128	512
Circotettix undulatus (Thomas), *rabula altior* Rehn	7	128	512
Circotettix thalassinus Saussure and *maculatus* Scudder	6-7	64-128	256-512
Aerochoreutes carlinianus strepitus Rehn	6-7	64-128	256-512
Bryodema tuberculatum bavaricum Zacher	7	128	512
Subfamily Acridinae			
Achurum sumichrasti Saussure	6	64	256
Mermiria m. maculipennis Bruner	6	64	256
Pedioscirtetes nevadensis Thomas, *maculipennis* (Scudder)	6	64	256
Mesochloa abortiva Bruner	6	64	256
Chorthippus longicornis (Latreille)	8	256	1024
Bruneria shastana Scudder	6	64	256
Cryptobothrus chrysophorus Rehn*	6	64	256

* Australian species.

members of the subfamily Acridinae which were studied, *Chorthippus longicornis* (Latreille) is peculiar in having eight generations of secondary spermatogonia. The cytoplasm of the spermatocytes is extremely reduced in this species, compared with a form such as *Bruneria,* in which the spermatocytes have a large amount of cytoplasm.

Within the genus *Trimerotropis,* the members of section A (White 1950) are characterized by six generations of spermatogonia. Some of the species in section B resemble them in this respect, but a group of species (*sparsa* (Thomas), *gracilis* (Thomas), *thalassica* Bruner, *cyaneipennis* Bruner, *caeruleipennis* Bruner) show seven generations. In certain members of the genus *Circotettix* and in the closely related *Aerochoreutes,* some cysts of primary spermatocytes contain 64 cells, others

128, the number of spermatogonial generations being apparently inconstant even within the individual.

III. Discussion

Systematic differences in the number of spermatogonial divisions have been reported in some Neuroptera by Suomalainen (1952) who states that the Hemerobiidae show six spermatogonial generations, the Chrysopidae only four to five. The adaptive significance of these different patterns of spermatogenesis in insects is obscure. In the case of cysts containing very many cells, synchronization of the stages of meiosis in all the cells within the cyst is often imperfect, but it is not clear whether such lack of synchronization is deleterious to the sperms in any way. Since the number of sperm bundles produced by an individual male certainly varies from species to species, the number of sperms per bundle is not a direct index of sperm production. However, it is clear that the small Morabinae produce far more sperms than many of the bulky Acrididae. The grasshoppers which produce the fewest sperms are probably some of the Oedipodinae and Acridinae with fountain type testes, relatively few follicles, and 256 sperms per bundle (rather than those Melanoplini with 64 or 128 sperms per bundle, since in these the number of bundles per follicle and the number of follicles per testis is greater). In general, the more archaic types of Acridoidea seem to have a greater sperm production than the more "modern" ones. But in no orthopteran has the production of sperm been reduced to anything like the extent found in the midge, *Miastor,* in which each male produces a total of exactly 1024 sperms (White 1946).

IV. Acknowledgments

The North American material included in Table 1 was collected with the aid of grants from the American Philosophical Society and the Research Institute of the University of Texas.

I am indebted to Dr. W. Jacobs of the University of Munich for the material of *Bryodema,* collected by him in Bavaria.

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AUSTRALIAN GENERA OF THE FAMILY PSYLLIDAE (HEMIPTERA: HOMOPTERA)

By L. D. TUTHILL* and K. L. TAYLOR†

(*Manuscript received November 25, 1954*)

Summary

An examination has been made of Froggatt's type specimens of Psyllidae, and an attempt made to bring his classification of the family into line with world fauna. All other genera known to occur in Australia are included in this revision. Species assigned to *Rhinocola* and *Aphalara* by Froggatt are now placed in *Creiis* Scott, *Eucalyptolyma* Froggatt, *Cardiaspina* Crawford, *Ctenarytaina* Ferris & Klyver, *Spondyliaspis* Signoret, and two new genera. Species placed in the genus *Psylla* Geoffroy by Froggatt are left undisturbed for the present, except that a new genus is erected for one species. Two new genera have been erected to receive the bulk of the species placed in *Trioza* Förster by Froggatt.

INTRODUCTION

The only appreciable work that has been done on the Psyllidae of Australia is that of Froggatt, who, in three principal papers (1900, 1901, 1903), named over 60 species and established nine new genera. Additional species were added to the list in 1923. Froggatt followed the system of generic arrangement which was in use at the time of his principal work, a system developed by Löw (1878) which was highly artificial, the genera being distinguished almost entirely on wing venational characters. Froggatt placed the Australian forms which he encountered within this framework wherever he could. In large measure this was erroneous. Since the work of Crawford (1914) and others has put the classification of this family on a different and more sound morphological basis it has been obvious to everyone interested in the family that Froggatt's work was in need of revision. For example, he placed a large number of species in *Rhinocola* and *Aphalara*, genera which apparently do not occur in Australia.

During a recent visit of the senior author to Australia it was possible for us to review Froggatt's material, which is housed in the Division of Entomology Museum, C.S.I.R.O., at Canberra, A.C.T. Although much of the material is in poor condition, the great majority of it is sufficiently well preserved to make identification certain. In addition, we have been able to examine some other material which has made possible additional clarification of generic relationships.

The present paper is intended to resolve some of the past error and present confusion at the generic level and thus provide a basis for future

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work. We are acutely aware that inasmuch as only a very small percentage of the psyllids of Australia are known many of the conclusions here presented will be found in need of revision in the future. Questions which we are unable to resolve are indicated in the discussion of the genera concerned.

Moreover, we are of the opinion that genera should be readily distinguishable on a morphologic basis and not erected for any and every group of related species. We would consider many such groups as subgenera. We know that this opinion is considered old-fashioned and is not followed by many present-day taxonomists who are more concerned with indicating relationships than with a system of classification that is useful to the non-specialist. We are herein purposely drawing the genera in broad terms both in respect of the above opinion and to allow for later refinement, where necessary, with the least possible confusion.

As Heslop-Harrison (1949*b*) pointed out in a comprehensive resumé of the published knowledge of the Australian psyllid fauna, a large segment of this fauna is entirely endemic and constitutes the core of a distinctive subfamily. Schwarz's (1898) name of Spondyliaspinae must be retained for this group although we wish it were not so, for *Spondyliaspis* is not a generalized or typical form but on the contrary is one of the most highly divergent types to be found within the subfamily. The particular character upon which Schwarz placed the most emphasis, the peculiar structure of the metatibiae and metatarsi, is actually found only in this one genus. Heslop-Harrison (1954) has recently published a definition of the subfamily Spondyliaspinae. We agree for the most part with his definitions, but inasmuch as a proper delimitation of the subfamilies of the Psyllidae is outside the scope of this paper and is being undertaken by him we are ignoring subfamily relations and limits. For the benefit of readers not familiar with the family, however, it is necessary to state what we consider are the principal characters of the Spondyliaspinae. These are: the absence of the meracanthi or caudal spurs on the metacoxae, which are swollen in a rather distinctive manner (in a majority of the genera which will be placed here, there is present a very small protuberance at the posterior edge of the metacoxal cavities. We do not consider these to be homologous with the meracanthi); the presence of a distinct terminal segment on the male proctiger; the peculiar linear type of venation of the forewing; the forewing with common medio-cubital petiole, with open pterostigma, *Rs* long and usually rather straight; the presence of a protruding lobe of the ocular sclerite between the eyes and the base of the antennae; the cylindrical or very broad, truncate genal processes; the broad flat pronotum which is similar to that found in the Aphalarinae.

KEY TO THE GENERA OF THE FAMILY PSYLLIDAE KNOWN TO OCCUR IN AUSTRALIA

1. Metacoxae with distinct meracanthi 11
Metacoxae more or less swollen but without meracanthi 2

2 (1). Forewings very long, narrow, with *Rs* parallel to costal margin, reaching apex of wing, thus strongly curved toward anal margin apically (see Figs. 1 and 2) 3
Forewings not extremely long and narrow, with *Rs* straight or more or less sinuate, curving to costal margin apically; if *Rs* reaching apex of wing genal processes very short 4

3 (2). Genal processes two-thirds as long as vertex or longer; tibia of metathoracic leg stout, shorter than femur or equal in length ....*Spondyliaspis* Signoret
Genal processes less than two-thirds as long as vertex; tibia of metathoracic leg slender, longer than femur ....*Eucalyptolyma* Froggatt

4 (2). Head wider than mesonotum; eyes recessive (see Fig. 10) 8
Head narrower than mesonotum; eyes rounded (see Fig. 3) 5

5 (4). Forewing with distinct subcostal vein, medial cell elongate, usually much longer than cubital 6
Forewing with subcosta completely fused with costa, medial cell not greatly elongate, more or less equal to cubital 7

6 (5). Thorax very strongly arched; forewing obliquely truncate, with apex toward anal margin ....*Lasiopsylla* Froggatt
Thorax moderately arched; forewing rounded or if somewhat truncate apex is toward costal margin ....*Creiis* Scott

7 (5). Antennae shorter than width of head or about as long ..*Cardiaspina* Crawford
Antennae longer than width of head (usually 1½ times as long or more) ....*Australopsylla*, gen. nov.

8 (4). Genal processes very short and broad, at least twice as broad as long, oblique to lateral point 9
Genal processes less than twice as broad as long, usually longer than broad ..10

9 (8). Antennae much shorter than width of head; costal margin of forewing deeply notched at base of pterostigma ....*Cometopsylla* Froggatt
Antennae longer than width of head; costal margin of forewing only slightly notched at base of pterostigma ....*Thea* Scott

10 (8). Antennae shorter than width of head; no prominent suture between lateral margin of vertex and ocular sclerite ....*Dasypsylla* Froggatt
Antennae longer than width of head; prominent suture separating lateral margin of vertex and ocular sclerite, eyes thus "stalked" ....*Scenitopsylla*, gen. nov.

11 (1). Media and cubitus of forewing with a common petiole 12
Media, cubitus, and radius of forewing arising at same point, or nearly so, from basal vein (see Fig. 20) 21

12 (11). Genae produced as distinct processes 13
Genae not produced as distinct processes 18

13 (12). Forewings with *Rs* curving parallel to costal margin, reaching apex of wing 14
Forewings with *Rs* straight or sinuate, not reaching apex of wing 15

14 (13). Genal processes short, broad ....*Eriopsylla* Froggatt
Genal processes long, slender, conical, smoothly continuous with vertex ....*Geijerolyma* Froggatt

15 (13). Forewings with *Rs* quite straight, *Rs*, *M*, and Cu_1 more or less parallel; mesotibia with preapical comb of setae (see Fig. 13) 16
Forewings otherwise; mesotibia without preapical comb of setae 17

16(15). Medial cell of forewing very small, shorter than cubital; proximal segment of metatarsus with claws .... *Ctenarytaina* Ferris & Klyver
Medial cell of forewing longer than cubital; proximal segment of metatarsus without claws .... *Syncarpiolyma* Froggatt
17(15). Antennae short, not longer than width of head; pterostigma lacking .... *Brachypsylla* Froggatt
Antennae longer than width of head; pterostigma usually present .... *Psylla* Geoffroy
18(12). Forewing without cross vein between *Rs* and furcation of *M* 19
Forewing with cross vein between *Rs* and furcation of *M* (see Fig. 18) ...20
19(18). Vertex not strongly excavate; *Rs* of forewing long, more or less straight .... *Aconopsylla*, gen. nov.
Vertex very deeply excavate between eyes; *Rs* of forewing short, curved to costa .... *Mycopsylla* Froggatt
20(18). R_1 of forewing running straight to costa, no pterostigma; *Rs* very short .... *Mesohomotoma* Kuwayama
R_1 of forewing forming a large, scarcely thickened pterostigma; *Rs* moderately long .... *Protyora* Kieffer
21(11). Anterior margin of vertex not sharp and overhanging nor produced as incurving lobes; metatibia with stout black apical spines ....*Trioza* Förster
Anterior margin of vertex either sharp and overhanging genal processes or produced as distinct lobes; metatibia with or without apical spines 22
22(21). Metatibia with apical spines; vertex produced anteriorly as distinct lobes .... *Schedotrioza*, gen. nov.
Metatibia without apical spines; anterior margin of vertex not produced as lobes but sharp and overhanging genal processes ..*Aacanthocnema*, gen. nov.

Genus SPONDYLIASPIS Signoret

Fig. 1

Spondyliaspis Signoret, 1879, Bull. (Ann.) Soc. Ent. Fr. (5)9: LXXXV.
Spondyliaspis Signoret, Schwarz 1898, Proc. Ent. Soc. Wash. 4: 68.

Type species *Spondyliaspis eucalypti* (Dobson), 1851 (= *Psylla eucalypti* Dobson) (original designation Schwarz 1898).

Head large, from narrower to slightly wider than mesonotum. Vertex flat, somewhat depressed discally. Ocular sclerite visible as distinct narrow section between vertex and eye, produced as small blunt lobe anteriorly. Genal processes large, from two-thirds as long as to longer than vertex, cylindrical, tapering, inner margin nearly straight, not touching, acute apically. Eyes large, rounded. Antennae much longer than width of head. Thorax rather flat. Pronotum long, quite flat, extending far down laterally to meet small propleura. Forewing very long, angulate apically; basal vein short; media and cubitus with short common petiole; subcosta present or absent, never strong; pterostigma present, at least partly closed, very long; *Rs* very long, reaching apex of wing, curved parallel to costal margin; marginal cells large, nearly equal. Legs short, all femora enlarged. Metacoxa swollen, without meracanthus. Metatibia shorter than or about equal to femur, enlarged apically with lateral protuberance bearing 2 black setae, another group of black setae on opposite margin. Proximal segment of metatarsus enlarged, somewhat spatulate, usually with only 1 small black claw, sometimes 2.

This, the type genus of the subfamily Spondyliaspinae, is highly specialized in many regards and is not typical of the endemic genera which will fall in that subfamily. It is most closely related to *Eucalyptolyma,* from which it differs in the much greater development of the genal processes, the more angulate forewing, and the remarkable metatibiae.

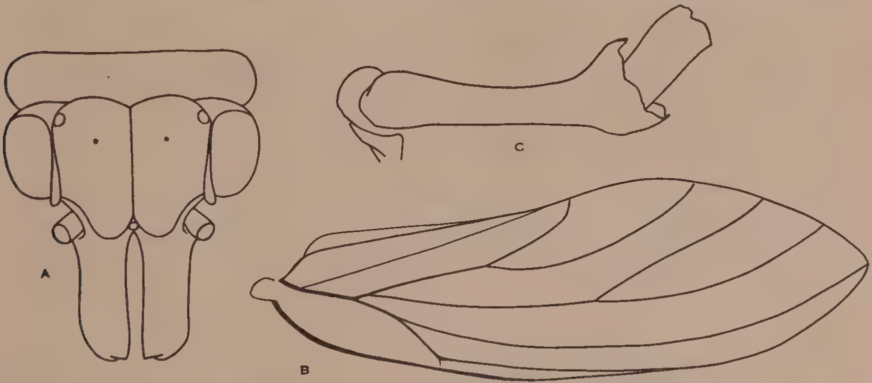

Fig. 1.—*Spondyliaspis* Signoret. *A,* head and pronotum; *B,* forewing; *C,* metatibia. (Based on undescribed species.)

In addition to the type species we place the following in this genus: *S. granulata* Froggatt, *S. hirsutus* Froggatt, *S. mannifera* Froggatt, *S. nigrocincta* Froggatt, *Aphalara flavilabris* Froggatt, and *S. occidentalis* Solomon. *Spondyliaspis rubra* Froggatt is assigned to *Creiis.* Type specimens of all these species except *S. occidentalis* Solomon and *S. eucalypti* (Dobs.) are in Froggatt's collection, Division of Entomology Museum, C.S.I.R.O., Canberra,* and have been examined. The location of the type of *S. occidentalis* Solomon is unknown.

Genus EUCALYPTOLYMA Froggatt

Fig. 2

Eucalyptolyma Froggatt, 1901, Proc. Linn. Soc. N.S.W. 26: 262.

Type species *Eucalyptolyma maideni* Froggatt, 1901 (original designation).

Head large, usually as broad as mesonotum or slightly broader, moderately deflected. Vertex flat, shallowly depressed discally. Ocular sclerite produced anteriorly as small lobe between eye and base of antenna, not visible between vertex and eye. Genal processes much shorter than

* Except where otherwise stated, all specimens mentioned hereafter are in the Division of Entomology Museum, C.S.I.R.O.

vertex, about as long as wide, cylindrical, divergent, rounded to more or less truncate apically. Eyes large, rounded to somewhat elongate and recessive. Antennae short, about as long as to $1\frac{1}{2}$ times width of head. Thorax quite flat dorsally. Pronotum quite flat, long, broad, extending far down laterally. Forewing long, narrow, usually rounded apically; basal vein very short; media and cubitus with short common petiole; subcosta not distinct; pterostigma present, long and narrow; *Rs* very long, following curve of costal margin to apex of wing; marginal cells small to moderate in size, more or less equal. Legs long. Metacoxa elongate, smooth, without meracanthus. Metatibia long, longer than femur, slender, with 2 groups of stout black setae on slightly flared apex. Proximal segment of metatarsus short, rounded, with 2 black claws.

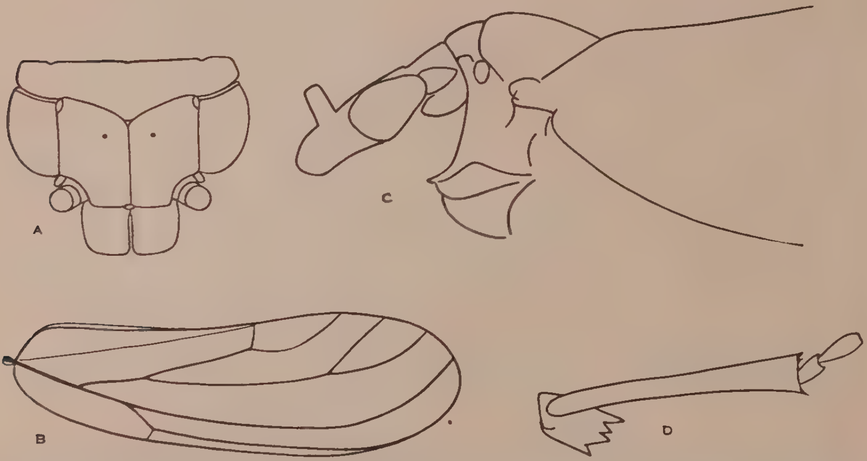

Fig. 2.—*Eucalyptolyma* Froggatt. *A*, head and pronotum; *B*, forewing; *C*, lateral aspect showing curvature of thorax; *D*, metatibia. (Based on undescribed species.)

In general habitus the species placed here resemble *Spondyliaspis* but differ markedly in the short genal processes, the long metatibia, and the rounded forewing.

In addition to *E. maideni* and *E. erratica* Froggatt we include the following in this genus: *Rhinocola assimilis* Froggatt, *R. nigripennis* Froggatt, *R. multicolor* Froggatt, and *Aphalara fuscipennis* Froggatt. Types of all six species are in Froggatt's collection and have been examined.

At least some of these species develop beneath the tests of various lerp-forming species, as commensals, between leaves tied together by caterpillars, and in other sheltered places.

Genus CREIIS Scott

Fig. 3

Creiis Scott, 1882, Trans. Ent. Soc. Lond. 1882: 462.

Type species *Creiis longipennis* (Walker), 1852 (= *Livia longipennis* Walker = *Psylla livioides* Walker) (original designation by Scott 1882).

Head narrower than mesonotum, somewhat deflected. Vertex flat, more or less depressed discally. Ocular sclerite only narrowly (if at all) visible between vertex and eye, ending as narrow protuberance anteriorly. Genal processes cylindrical, stout, contiguous or nearly so, rounded apically. Eyes rounded, not recessive. Antennae long, usually more than 1½ times as long as width of head. Thorax rather flat dorsally. Pronotum long, broad, strongly arched. Forewing elongate, narrowly rounded apically; media and cubitus with common petiole; subcosta distinct, forming narrow closed cell with costa; pterostigma present, open; *Rs* long, curved toward costa apically, nearly straight; marginal cells large, elongate, medial longer than cubital. Legs stout, all femora much enlarged. Metacoxa swollen, smooth, without meracanthus. Metatibia flaring apically, with several stout black setae in 2 distinct groups. Two small claws present on proximal segment of metatarsus.

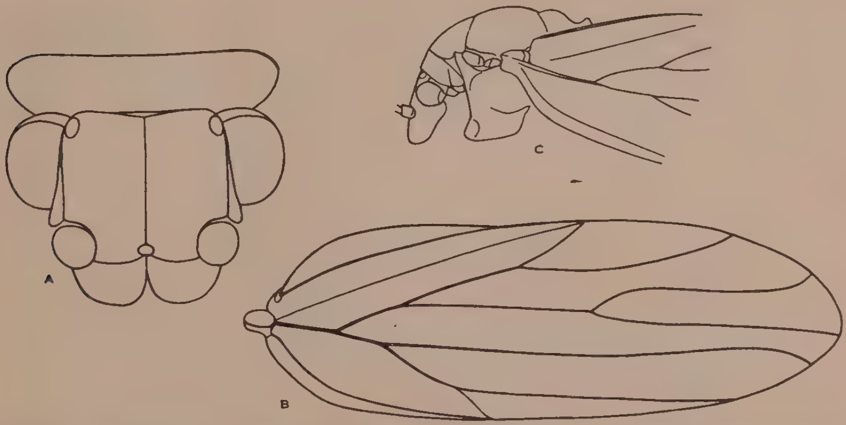

Fig. 3.—*Creiis* Scott. *A*, head and pronotum; *B*, forewing; *C*, lateral aspect showing curvature of thorax. (Based on *C. longipennis* (Walker).)

The most distinctive characters of this genus are the distinct subcosta and the elongate medial cell of the forewing.

Additional species placed here are *Rhinocola viridis* Froggatt, *R. corniculata* Froggatt, *R. liturata* Froggatt, *R. costatus* Froggatt, *Lasiopsylla pellucida* Froggatt, and *Spondyliaspis rubra* Froggatt. Froggatt's collection includes type specimens of the first three species, but only adults and lerps of *R. costatus* and *S. rubra* and only lerps of *L.*

pellucida, all named by him. Lerps recently collected (Sutton Road, A.C.T., 18.xii.1952, E. Lewis) appear to be identical with Froggatt's specimen (New South Wales Department of Agriculture collection) of *L. pellucida* illustrated by Zeck (Froggatt 1923, col. pl.) and the associated adults are clearly *Creiis*. The type of *C. longipennis* in the British Museum (Scott 1882) has not been examined.

Genus LASIOPSYLLA Froggatt

Fig. 4

Lasiopsylla Froggatt, 1900, Proc. Linn. Soc. N.S.W. 25: 261.

Type species *Lasiopsylla rotundipennis* Froggatt, 1900 (original designation).

Head large, narrower than mesonotum, vertical. Vertex flat, more or less depressed discally, nearly square. Ocular sclerite not visible between vertex and eye, anteriorly produced as angular protuberance. Genal processes stout, slightly constricted at base, rounded. Eyes rounded, not recessive. Antennae long, over 1½ times as long as width of head. Thorax very strongly arched at front margin of scutum so that prescutum, pronotum, and vertex are in line and at almost 90° to axis of rest of body. Pronotum long, broad, flat. Forewing elongate, more or less obliquely truncate apically from costa to between M_2 and Cu_1; media and cubitus

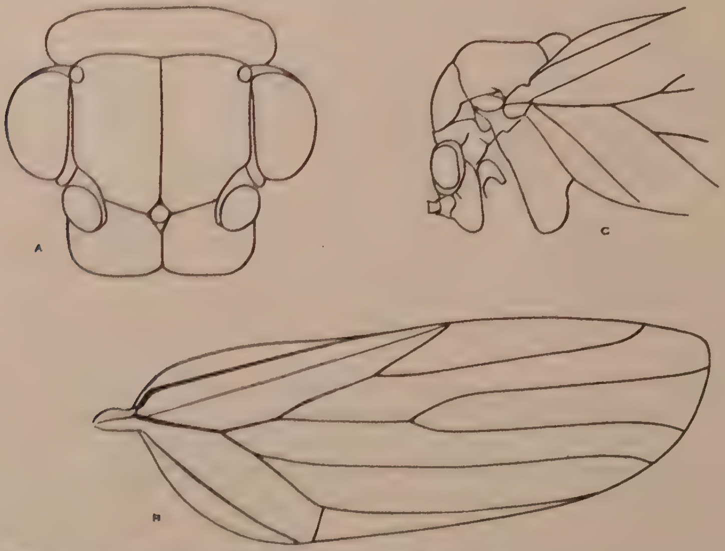

Fig. 4. *Lasiopsylla* Froggatt. *A*, head and pronotum; *B*, forewing; *C*, lateral aspect showing curvature of thorax. (Based on *L. rotundipennis* Frogg.)

with common petiole; subcosta distinct, forming narrow closed cell with costa; pterostigma present, open; *Rs* long, curved toward costa apically; marginal cells large, very elongate, medial slightly longer than cubital. Legs stout, all femora enlarged. Metacoxa without meracanthus. Metatibia robust, shorter than femur, flaring apically, with 2 groups of black spines. Proximal segment of metatarsus with minute claws or none.

Lasiopsylla rotundipennis and *L. bullata* Froggatt are quite distinctive in the very strongly arched thorax, and the extremely long medial cell. The forewing of both species is truncate. Thus the differences between *Lasiopsylla* and *Creiis* are of degree more than character and it seems probable that with more complete knowledge of the Australian species it will be necessary to synonymize the genera.

L. pellucida, *L. striatus*, and *L. falcatus* were named by Froggatt from the lerps only. *L. pellucida* Froggatt is here assigned to *Creiis*. Froggatt's collection includes lerps of *L. falcatus* but no adults, and no other material is available. Specimens recently collected (Waite Institute, S.A., 19.x.1951, I.F.B. Common) appear to correspond with Zeck's illustration of *L. striatus* (Froggatt 1923, col. pl.) and the adults belong to *Lasiopsylla*.

Genus CARDIASPINA Crawford

Fig. 5

Cardiaspina **Crawford, 1911, Pomona Coll. J. Ent. 3: 632.**

Cardiaspis Schwarz, 1898 (non Amyot 1846), Proc. Ent. Soc. Wash. 4: 72.

Pennapsylla Froggatt, 1923, Forest Ins. Austral., col. pl. (nomen nudum).

Type species *Cardiaspina artifex* (Schwarz), 1898 (original designation Crawford 1911).

Head narrower than mesonotum, vertical. Vertex flat, depressed discally. Ocular sclerite visible as small lobe between eye and base of antenna. Genal processes stout, swollen, obliquely truncate, more or less contiguous. Eyes rounded, not recessive. Antennae short, shorter than or about as long as width of head. Thorax rather flat except anteriorly curved down to head. Pronotum long and broad. Forewing long, narrowly rounded apically; media and cubitus with common petiole; no distinct subcosta; small open pterostigma present; *Rs* nearly straight, reaching nearly to apex of wing; marginal cells short, triangulate, nearly equal. Legs stout, femora enlarged. Metacoxa swollen, without meracanthus. Metatibia flaring apically, with continuous row of spines around anterior half. Claws on proximal segment of metatarsus very small or absent.

Members of this genus are of a distinctive habitus which serves to distinguish them readily from most of the others known. The body is relatively short and robust. The combination of a vertical head, narrower than the mesonotum, and the short antennae combine to separate it from those most similar to it.

Species placed here in addition to the type are *C. textrix* Froggatt, *C. rubra* Froggatt, *C. vittaformis* Froggatt, *C. brunneus* Froggatt, *C. spiniferus* Froggatt, *Pennapsylla alba* Froggatt, and *Rhinocola pennaeformis* Froggatt. *C. plicatuloides* Froggatt is placed in the new genus *Scenitopsylla.*

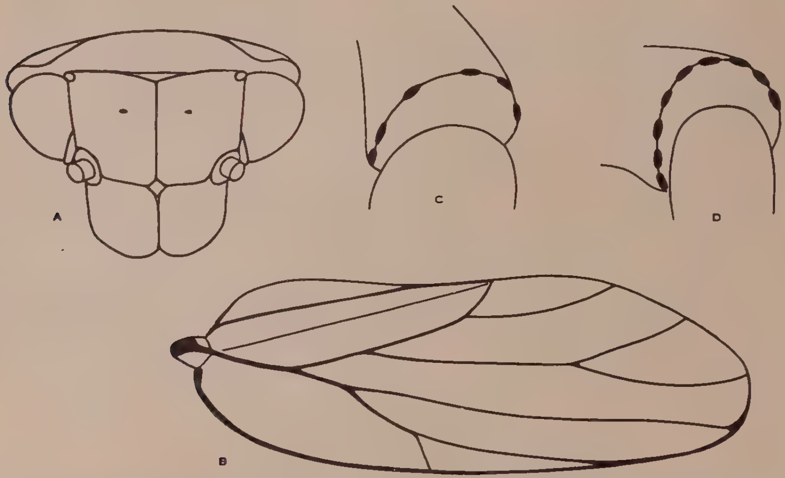

Fig. 5.—*Cardiaspina* Crawford. *A, C. artifex* (Schwarz) — head and pronotum; *B, C. artifex* (Schwarz) — forewing; *C, D,* apex of metatibia in two different species.

The type of *C. artifex* is in the U.S. National Museum, Washington (Schwarz 1898) and specimens (The Spit, N.S.W., 17.ix.1953, E. Lewis) have been compared with it. Froggatt's types of *C. textrix, C. rubra,* and *R. pennaeformis* have been examined, and his collection also includes an adult specimen and lerp of *P. alba* named by him. The lerp specimens of *C. spiniferus* and *C. brunneus* illustrated by Zeck (Froggatt 1923, col. pl.) are in the New South Wales Department of Agriculture collection and have been compared with material recently collected. Adult specimens (Tharwa Road, A.C.T., 23.x.1954, E. Lewis) bred from lerps identical with those of *C. spiniferus* clearly fall in this genus, as also do specimens (15 miles south of Gundagai, N.S.W., 18.ix.1954, E. Lewis) bred from lerps almost identical with those of *C. brunneus.*

Genus AUSTRALOPSYLLA, gen. nov.
Fig. 6

Type species *Australopsylla revoluta* Froggatt, 1900 (= *Rhinocola revoluta* Froggatt) (here designated).

Head equal to or narrower than mesonotum, strongly deflected, vertical or nearly so. Vertex flat, more or less depressed discally. Ocular sclerite developed as distinct lobe between eye and antenna, usually visible between eye and vertex. Genal processes cylindrical, stout, obliquely truncate, contiguous or nearly so. Eyes rounded, or slightly recessive. Antennae distinctly longer than width of head, usually 1½ times as long or more. Thorax broad, rather flat dorsally. Pronotum short, rather narrow. Forewing rounded apically; basal vein very short, media and cubitus with common petiole; no distinct subcosta; pterostigma present, open or partly closed by spur of R_1; *Rs* long, nearly reaching apex of wing, moderately curved; marginal cells large, cubital larger than medial. Legs stout. Metacoxa swollen, without meracanthus. Metatibia flaring apically, with several black setae in 2 groups.

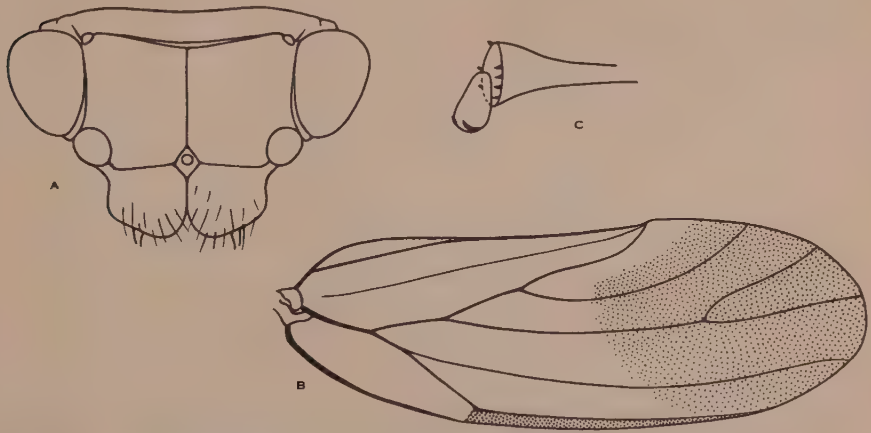

Fig. 6.—*Australopsylla*, gen. nov. *A*, head and pronotum; *B*, forewing; *C*, apex of metatibia. (Based on undescribed species.)

This genus lies between *Creiis* and *Cardiaspina*. As constituted here it serves to include species which it will probably be necessary to segregate into additional genera when the fauna is better known. It seems to us inadvisable to establish numerous genera at this time while the outlines of group relationships are so nebulous.

In addition to *A. revoluta* we place here *Rhinocola marmorata* Froggatt and *Aphalara carinata* Froggatt. Types of all three species are in Froggatt's collection.

The name *Australopsylla* is derived from the Latin australis (= south) + *Psylla*.

Genus THEA Scott

Fig. 7

Thea Scott, 1882, Trans. Ent. Soc. Lond. 1882: 450.

Type species *Thea trigutta* (Walker), 1858*a* (= *Psylla trigutta* Walker) (original designation Scott 1882).

Head large, wider than mesonotum, very strongly deflected. Vertex broad, depressed discally, somewhat swollen anteriorly. Ocular sclerite only visible anteriorly between vertex and eye, produced as large lobe between eye and base of antenna. Genal processes very short and broad, oblique from inner margin to lateral edge. Eyes elongate, recessive. Antennae equal to or longer than width of head. Thorax broad, rather flat. Pronotum flat, very long and wide, as wide as mesonotum, extending far down laterally. Proepimeron often hidden or very small, completely ventral in orientation. Forewing very narrowly rounded or obliquely truncate to rounded apex; costal margin with distinct break or notch at base of pterostigma; media and cubitus with common petiole; no distinct subcosta; pterostigma present, short, very broad; *Rs* long, reaching or almost reaching apex of wing, slightly sinuate; marginal cells variable. Legs stout, femora swollen, especially those of mesothorax. Metacoxa swollen, without meracanthus. Metatibia long, slightly enlarged apically, with several small black setae on anterior margin. Proximal segment of metatarsus with 2 small black claws.

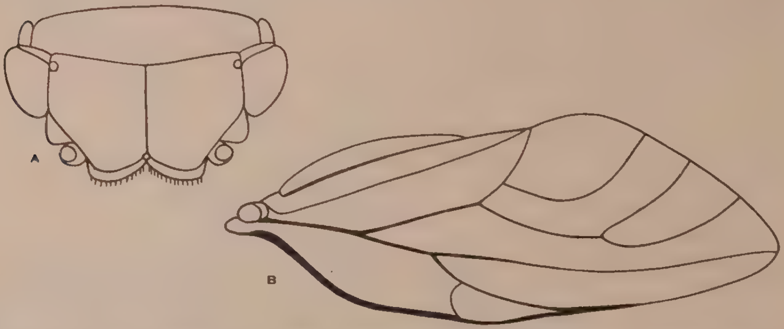

Fig. 7.—*Thea* Scott. *A*, head and pronotum; *B*, forewing. (Based on *T. formicosa* Froggatt.)

The very peculiar form of the genal processes and the broad head serve to distinguish this genus from all others except *Cometopsylla*, which is very closely related.

The place of origin of the type species is unknown (see Scott 1882, p. 453) but is almost certainly Australia. Confirmation of this must await demonstrated identity of specimens from a known locality with the type in the British Museum.

Species placed here, other than the type, are *T. formicosa* Froggatt, *T. opaca* Froggatt, *T. leai* Froggatt, *T. olivacea* Froggatt, and *T. wellingtoniae* Froggatt. Walker's type of *P. trigutta* is in the British Museum (Scott 1882). Types of the remaining five species are in Froggatt's collection.

Genus COMETOPSYLLA Froggatt

Fig. 8

Cometopsylla Froggatt, 1900, Proc. Linn. Soc. N.S.W. 25: 286.

Type species *Cometopsylla rufa* Froggatt, 1900 (original designation).

Head large, very broad, wider than mesonotum, strongly deflected, nearly vertical. Vertex broad, flat. Ocular sclerite not distinct between eye and vertex, produced as large bulbous lobe between eye and base of antenna. Genal processes extremely short and broad, oblique to lateral angles. Eyes elongate, strongly recessive, touching mesepisternum. Antennae very short, much shorter than width of head. Thorax broad, flat dorsally. Pronotum nearly vertical, long, wide, extending far down laterally. Forewing short, broad, roundly oblique to narrowly rounded apex; membrane thickened; costa with deep notch at base of pterostigma; media and cubitas with common petiole; no distinct subcosta; pterostigma present, open, broad and long, tapering well toward tip of wing; *Rs* nearly straight, slightly curved toward costa apically; marginal cells small, nearly equal. Legs short, stout. Mesothoracic femora greatly swollen, twisted, deeply grooved for reception of flexed tibia. Pro- and metathoracic femora less strongly swollen, also grooved but less extensively. Metacoxa without meracanthus. Metatibia with row of stout black setae around anterior portion of slightly enlarged apex. Proximal segment of metatarsus with pair of strong black claws.

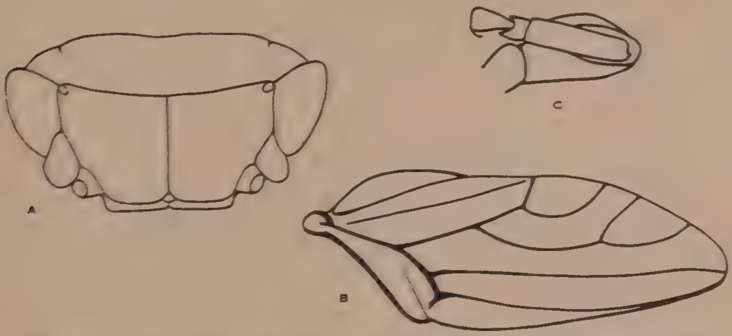

Fig. 8.—*Cometopsylla* Froggatt. *A*, head and pronotum; *B*, forewing; *C*, mesothoracic leg. (Based on *C. rufa* Froggatt.)

The type and only species (type in Froggatt's collection) placed here is simply an extreme form of the type of *Thea*. It is possible that future collections will make it necessary to place it in that genus but this seems unlikely. It differs from *Thea* in the very short antennae, the deeper notch on the costa at the base of pterostigma, and the peculiar mesothoracic femora.

Genus DASYPSYLLA Froggatt

Fig. 9

Dasypsylla Froggatt, 1900, Proc. Linn. Soc. N.S.W. 25: 293.
Callistochermes Kirkaldy, 1905, Canad. Ent. 37: 291.

Type species *Dasypsylla brunnea* Froggatt, 1900 (original designation).

Head very large, much broader than mesonotum, nearly vertical to axis of body. Vertex broad, deeply depressed discally. Ocular sclerite narrowly but distinctly visible between vertex and eye, produced as broad blunt lobe between eye and base of antenna. Genal processes broad, as long as broad, strongly constricted at base. Eyes elongate, recessive. Antennae about equal to width of head. Thorax very strongly arched. Pronotum rather short, nearly vertical. Proepimeron swollen, much larger than proepisternum. Forewing large, broadly rounded apically; media and cubitus with common petiole; subcosta distinct, forming a long narrow cell with costa; pterostigma present, small; *Rs* long, somewhat sinuate, curved toward costa apically; marginal cells moderately large, broad. Legs stout, all femora enlarged. Metacoxa swollen, without meracanthus. Metatibia with several black setae in 2 distinct groups on enlarged apex. Proximal segment of metatarsus with 2 small black claws.

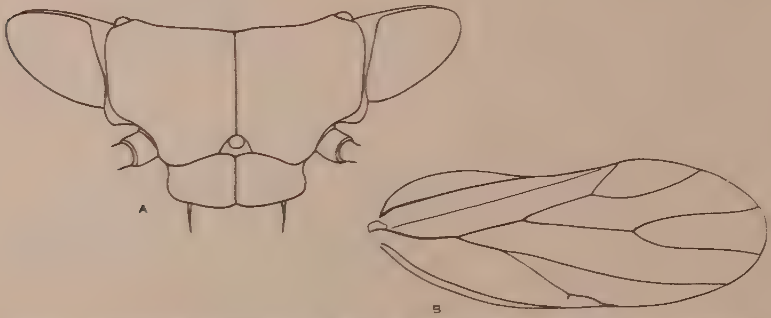

Fig. 9.—*Dasypsylla* Froggatt. *A*, head; *B*, forewing. (Based on *D. brunnea* Froggatt.)

The type specimen of *D. brunnea* is in Froggatt's collection. The type specimen of *Callistochermes rubrovariegata* Kirkaldy is in the collection of the Hawaiian Sugar Planters' Experiment Station in Honolulu and has been examined by the senior author. It is certainly congeneric with and is identical with specimens of *D. brunnea* at hand except in some minor points such as somewhat more slender antennae and a somewhat lighter colour. All the specimens available are somewhat teneral. With some doubt therefore *rubrovariegata* is placed as a synonym of *brunnea*.

No other species are known.

Genus SCENITOPSYLLA, gen. nov.

Fig. 10

Type species *Scenitopsylla plicatuloides* (Froggatt), 1900 (= *Cardiaspis plicatuloides* Froggatt) (here designated).

Head short, wider than mesonotum, vertical. Vertex more or less depressed discally, somewhat swollen anteriorly. Ocular sclerite very strongly developed between vertex and eye, eyes thus definitely "stalked". Eyes elongate and strongly recessive. Genal processes short to moderately long, cylindrical, obliquely truncate, somewhat constricted at base. Antennae longer than width of head (usually 1½ times as long or more). Thorax broad, strongly arched. Pronotum narrow, moderately long, vertical. Forewing broad, rounded apically; media and cubitus with common petiole; subcosta fused with costa or distinct; pterostigma present, open; *Rs* slightly sinuate, turned toward costa at apex; marginal cells of moderate size, medial longer than cubital. Legs short, stout. Femora enlarged, especially mesothoracic, short, swollen, curved, grooved toward apex to receive base of tibia. Metacoxa enlarged, without meracanthus. Metatibia enlarged apically, with several stout black setae in 2 distinct groups. Proximal segment of metatarsus without black claws.

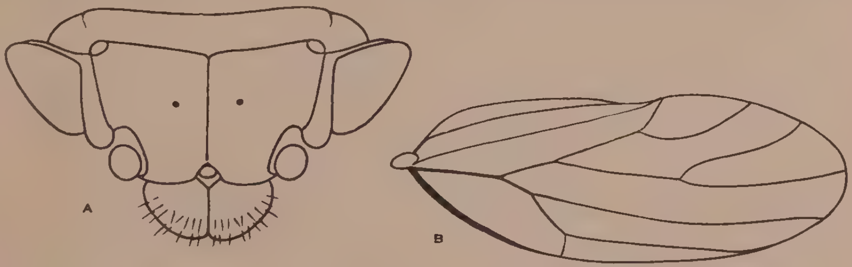

Fig. 10.—*Scenitopsylla*, gen. nov. *A*, head and pronotum; *B*, forewing. (Based on *S. nigra* (Froggatt).)

The species placed here show relationships to *Dasypsylla*, from which they may be distinguished readily by the long antennae and the short robust body. The general habitus is that of *Cardiaspina*, with which they will easily be confused in the field. The long antennae, the very broad head, and elongate, recessive, stalked eyes, however, separate them sharply from *Cardiaspina*.

In addition to *plicatuloides* we place *Rhinocola nigra* Froggatt, *R. mollis* Froggatt, and *R. ostreata* Froggatt here. Froggatt's collection includes type specimens of *C. plicatuloides* and *R. ostreata*, and lerp specimens (named by him) of *R. nigra*. We have a specimen (Tharwa Road, A.C.T., 20.x.1953, K. L. Taylor) of which the lerp is identical with Froggatt's and the adult undoubtedly belongs in this genus. The lerp specimen of *R. mollis* (New South Wales Department of Agriculture Collection) from which Zeck prepared his illustration (Froggatt 1923, col. pl.) has been compared and is considered identical with a new specimen (Black Mt., A.C.T., 30.iii.1953, E. Lewis) of which the adult is available.

The name *Scenitopsylla* is derived from the Greek σκηνιτης (= tent dweller or tent maker) + *Psylla.*

Genus ERIOPSYLLA Froggatt

Fig. 11

Eriopsylla Froggatt, 1901, Proc. Linn. Soc. N.S.W. 26: 266.

Type species *Eriopsylla viridis* Froggatt, 1901 (original designation).

Head large, broad, as broad as mesonotum. Vertex somewhat depressed discally, long, curving down anteriorly to short, broad, flat genal processes. Eyes rounded, not recessive. Antennae slightly longer than width of head. Thorax flat dorsally. Pronotum long, broad, flat. Forewing elongate, rounded apically; pterostigma weak, open; media and cubitus with common petiole; *Rs* long, curved parallel to costa, reaching apex of wing; marginal cells long, narrow. Legs stout, femora enlarged. Metacoxa with blunt meracanthus. Metatibia short, with several apical setae. Proximal segment of metatarsus without claws.

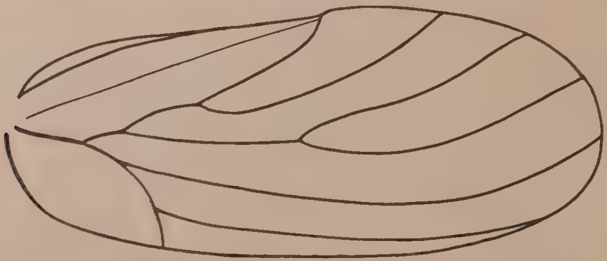

Fig. 11.—*Eriopsylla* Froggatt, forewing. (Based on *E. viridis* Froggatt.)

The unique type specimen (Froggatt's collection) of *viridis* is in such poor condition that much of its exact structure is indeterminable but it appears to be distinct as indicated. The short broad genal processes serve to separate it at once from *E. gracilis,* which Froggatt originally placed here but subsequently moved to *Aphalara* and which we are assigning to *Ctenarytaina.* The forewings are somewhat as in *Eucalyptolyma.*

Genus GEIJEROLYMA Froggatt

Fig. 12

Geijerolyma Froggatt, 1903, Proc. Linn. Soc. N.S.W. 28: 335.

Type species *Geijerolyma robusta* Froggatt, 1903 (original designation).

Head large, broad, as broad as mesonotum. Vertex not flat, raised above antennae, curving down anteriorly. Genal processes long, longer than vertex, conical, contiguous, smoothly continuous with vertex. Eyes hemispherical. Antennae very long. Thorax flat dorsally. Pronotum long, broad, slightly curved. Forewing long, broad, acutely rounded apically; costal margin evenly arcuate throughout its length; costa thickened at base; basal vein short; media and cubitus with common petiole; no pterostigma present; *Rs* long, curved parallel to curved costal margin, reaching apex of wing; *M* + *Cu* and cubital petiole both very short; marginal cells large. Legs stout, all femora enlarged. Metacoxa with small blunt meracanthus. Metatibia flaring slightly apically with several stout black setae. Proximal segment of metatarsus with 2 black claws.

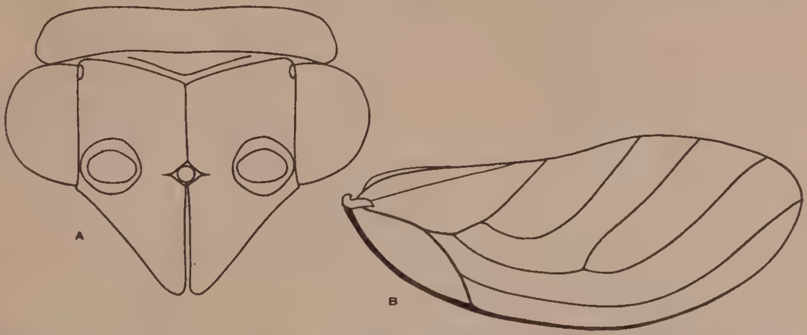

Fig. 12.—*Geijerolyma* Froggatt. *A*, head and pronotum; *B*, forewing. (Based on *G. robusta* Froggatt.)

Froggatt's interpretation of the head structure of the unique species *G. robusta* led him to place it near *Tyora*. However, it has all the characters of the Psyllinae, being distinctive only in the genal processes and the forewing. Froggatt's type specimens (in his collection) have been examined.

Genus CTENARYTAINA Ferris & Klyver

Fig. 13

Ctenarytaina Ferris & Klyver, 1932, Trans. Proc. N.Z. Inst. 63: 54.

Type species *Ctenarytaina fuchsiae* (Maskell), 1890 (= *Rhinocola fuchsiae* Maskell) (original designation Ferris and Klyver 1932).

Head large, distinctly broader than mesonotum, nearly vertical to axis of body. Vertex depressed discally, strongly bulging and rounded down anteriorly, curving smoothly to genal processes without distinct suture. Small lobe of ocular sclerite visible between eye and base of antenna. Genal processes short blunt, contiguous or separated. Eyes recessive, more or less elongate. Antennae about as long as width of head. Thorax broad, short, and quite flat dorsally. Pronotum very broad, as broad as mesonotum or broader, moderately long. Forewing long, narrow, rounded apically, membrane somewhat thickened, retecious; break in costa at base of pterostigmal thickening; pterostigma with or without distinct marginal vein, long, slender; basal vein extremely short; media and cubitus with common petiole; *Rs* very long, straight to near tip, nearly reaching apex of wing; media long, straight to small, broad cell at apex of wing; cubitus short, cubital cell rather large, larger than medial; Cu_1 more or less parallel to media and *Rs*. Legs of moderate size. Mesotibia with preapical comb of small setae. Metacoxa with prominent, elongate, blunt meracanthus. Metatibia with several prominent black setae at apex. Proximal segment of metatarsus with small claws.

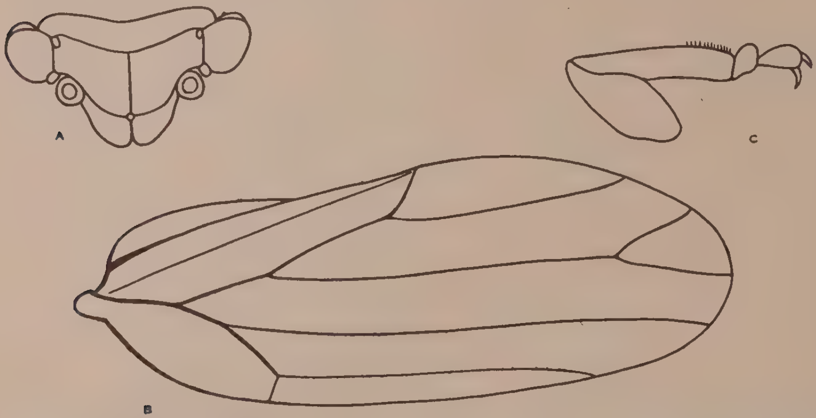

Fig. 13.—*Ctenarytaina* Ferris & Klyver. *A*, head and pronotum; *B*, forewing; *C*, mesotibia. (Based on undescribed species.)

The type species is native to New Zealand but a number of Australian species are congeneric with it. Of the species described from New Zealand by Ferris and Klyver *C. thysanura* is certainly of Australian origin although it has not been recorded from Australia. Its host is *Boronia* sp., used as an ornamental in New Zealand. *Rhinocola eucalypti* Maskell is properly placed here as indicated by Tuthill (1952). Additional species placed here are *Aphalara obscura* Froggatt and *Aphalara gracilis* (Froggatt). Froggatt's collection includes the type of *A. gracilis* (still labelled *Eriopsylla*), but only named specimens of *A. obscura* (det. Froggatt). The location of the type is unknown.

Genus SYNCARPIOLYMA Froggatt

Fig. 14

Syncarpiolyma Froggatt, 1901, Proc. Linn. Soc. N.S.W. 26: 269.

Type species *Syncarpiolyma maculata* Froggatt, 1901 (original designation).

Head large, very broad, broader than mesonotum, nearly vertical to axis of body. Vertex strongly narrowed anteriorly, depressed discally. Genal processes short, broad, rounded, contiguous. Small lobe of ocular sclerite visible between eye and base of antenna. Eyes very large, elongate, distinctly recessive. Antennae short, less than width of head. Thorax broad, rather flat dorsally, sharply deflected anteriorly. Pronotum nearly vertical, long, broad, triangular. Forewing elongate, rounded apically; basal vein very short; media and cubitus with common petiole; pterostigma absent or very weak; *Rs* straight, long, reaching nearly to apex of wing; marginal cells of moderate size, narrow, medial larger than cubital. Mesotibia with preapical comb of small setae. Metacoxa with small but distinct meracanthus. Metatibia very long and slender with several stout black setae at apex. Proximal segment of metatarsus without claws.

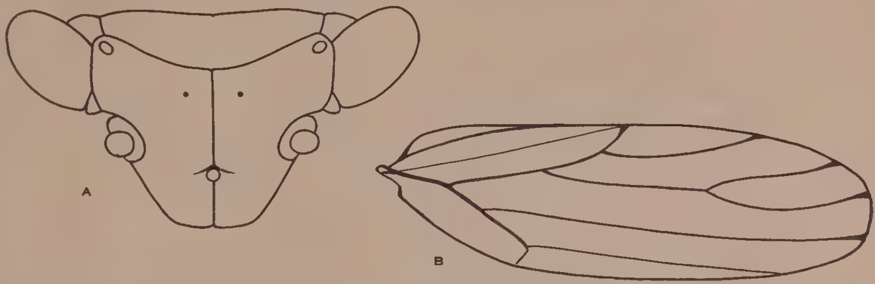

Fig. 14.—*Syncarpiolyma* Froggatt. *A*, head and pronotum; *B*, forewing. (Based on *S. maculata* Froggatt.)

The single species placed here shows definite relationship to *Ctenarytaina* but differs in the structure of the head, in the form and size of the marginal cells of the forewing, and in the lack of claws on the proximal segment of the metatarsus. The type of *S. maculata* is in Froggatt's collection.

Genus BRACHYPSYLLA Froggatt

Fig. 15

Brachypsylla Froggatt, 1901, Proc. Linn. Soc. N.S.W. 26: 270.

Type species *Brachypsylla tryoni* Froggatt, 1901 (original designation).

Head narrower than mesonotum. Vertex flat, depressed discally. Genal processes broadly conical. Eyes rounded. Antennae stout, short, shorter than width of head. Thorax rather flat dorsally. Pronotum broad, wide, flat. Forewing broad, short, broadly rounded, veins strong; media and cubitus with common petiole; costa very thick, broad, broad where R_1 joins but no true pterostigma; *Rs* slightly sinuate, curving up towards costal margin apically; marginal cells of moderate size, more or less equal. Legs stout. Metacoxa with small conical meracanthus. Metatibia long, with several long black apical setae. Proximal segment of metatarsus with pair of black claws.

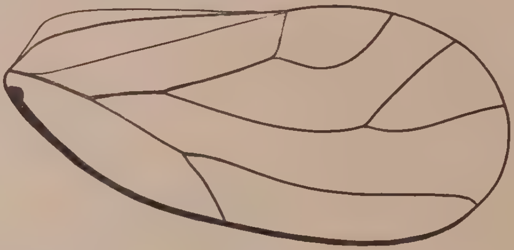

Fig. 15.—*Brachypsylla* Froggatt, forewing. (Based on *B. tryoni* Froggatt.)

The unique type species (type in Froggatt's collection) is distinct from related forms known, and referred to *Psylla,* in the very short antennae. The lack of a pterostigma and the long metatibiae are also unusual.

Genus PSYLLA Geoffroy

Type species *Psylla alni* (Linn.), 1758 (= *Chermes alni* Linn.) (original designation Geoffroy 1762).

With two or three possible exceptions the Australian species that have been placed in *Psylla* can be included in this genus only if the generic limits are stretched severely. Heslop-Harrison (1949*a*) established the genus *Neopsylla** Heslop-Harrison (non *Neopsylla* Wagner, 1903) for several of the species. The species available to us show great variation, especially in head and thoracic characters. Many species on hand are undescribed and certainly there are a great many more to be collected. We are therefore of the opinion that an attempt at establishing segregates, whether genera or subgenera, at this time would be premature and would almost certainly be the source of considerable later confusion. We are therefore leaving undisturbed, for the present, all the species assigned to *Psylla* by Froggatt with the exception of *P. sterculiae* for which a new genus is erected.

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* The name *Acizzia* was indicated as a substitute for *Neopsylla* Heslop-Harrison in an informal manner in 1951 (Heslop-Harrison 1951, p. 417). So far as we are aware this substitution of *Acizzia* for *Neopsylla* has not been proposed in a manner which is valid under the International Rules of Zoological Nomenclature and thus stands as a nomen nudum.

Froggatt's collection includes the types of *P. acaciae-baileyanae, P. acaciae-decurrentes, P. acaciae-pendulae, P. acaciae-pycnanthae, P. candida, P. capparis, P. frenchi,* and *P. schizoneuroides,* but only named specimens (det. Froggatt) of *P. acaciae-dealbatae, P. acaciae-juniperinae,* and *P. gracilis.*

Genus ACONOPSYLLA, gen. nov.

Fig. 16

Type species *Aconopsylla sterculiae* (Froggatt), 1901 (= *Psylla sterculiae* Froggatt) (here designated).

Head broad, about as wide as mesonotum. Vertex rounded, curving down strongly anteriorly, fused with genae. Genae not produced as processes. Frons greatly enlarged, completely visible. Eyes rounded. Antennae about equal to width of head. Thorax quite flat dorsally. Pronotum long, broad, curved. Forewing broad, rounded apically; costa thickened at base; media and cubitus with common petiole; pterostigma present, long and narrow; *Rs* long, curving slightly towards costal margin; medial cell small, triangular, cubital larger. Legs stout, all femora enlarged. Metacoxa with small meracanthus. Metatibia with several black setae at apex. Proximal segment of metatarsus without claws.

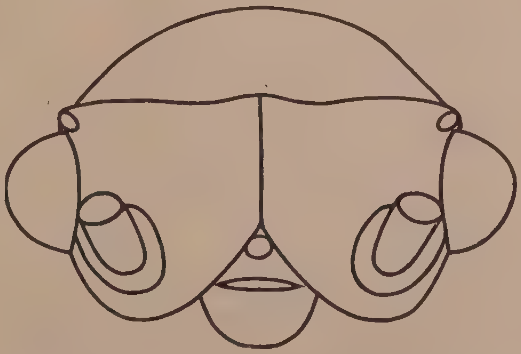

Fig. 16.—*Aconopsylla*, gen. nov., head and pronotum. (Based on *A. sterculiae* (Froggatt).)

The only species placed here (type in Froggatt's collection) differs greatly from *Psylla* in the morphology of the head, principally in the genae and the very short antennae.

The name *Aconopsylla* is derived from the Greek negative prefix *a* + κωνος (= cone) + *Psylla,* in reference to the lack of genal processes or cones.

Genus MYCOPSYLLA Froggatt

Fig. 17

Mycopsylla Froggatt, 1901. Proc. Linn. Soc. N.S.W. 26: 258.

Type species *Mycopsylla fici* (Tryon), 1894 (= *Psylla fici* Tryon) (original designation Froggatt 1901).

Head narrower than mesonotum. Vertex very deeply excavate medially, strongly raised laterally above level of eyes. Lateral ocelli above eyes. Genae not produced, flat, long, touching or nearly touching, frons thus covered except for very narrow strip below median ocellus. Eyes very large, rounded. Antennae large, very long, much longer than width of head. Thorax strongly arched. Pronotum large, nearly as broad as mesonotum, medially vertical and much depressed below vertex, laterally fused with propleura forming large lobe which extends back nearly to mesonotum. Metanotum produced as 2 truncate dorsal processes. Forewing large, membranous, angulate apically; costa narrow; basal vein short, strongly sinuate; media and cubitus with very short common petiole; pterostigma present, large, closed, opaque; *Rs* short, curved to costa; medial cell narrow, paralleling costa, including apex of wing, cubital cell very large. Cu_1 approaching base of *M*. Legs large, long. Metacoxa smoothly curved, with large, sharp meracanthus. Metatibia with corona of heavy black spines apically. Proximal segment of metatarsus with 2 black claws, large plantar vesicle.

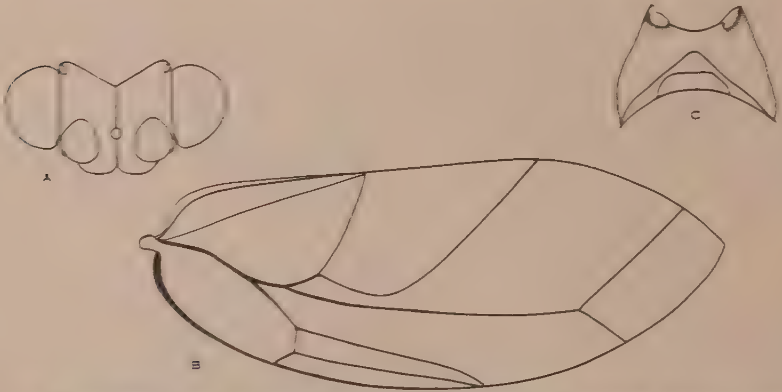

Fig. 17.—*Mycopsylla* Froggatt. *A*, head; *B*, forewing; *C*, paired processes on 2nd abdominal tergite. (Based on *M. proxima* Froggatt.)

Other than the type, *M. proxima* Froggatt is the only species known. Type specimens of both species are in Froggatt's collection. The relationships of these two species are not apparent as yet because of lack of knowledge of the tropical psyllid fauna of the world. *Mycopsylla* seems to belong to the Pauropsyllinae of Crawford on the basis of head and wing characters and is perhaps most closely related to *Macrohomotoma* Kuwayama. In a number of ways it is reminiscent of the central and South American genus *Synoza.* The paired dorsal processes on the metanotum are more strongly developed in *M. proxima* than in *M. fici.*

Genus MESOHOMOTOMA Kuwayama

Fig. 18

Mesohomotoma Kuwayama, 1907, Trans. Sapporo Nat. Hist. Soc. 2: 180.

Udamostigma Enderlein, 1910, Wissensch. Ergeb. der Schwed. Zool. Exped. nach Dem Kilimandjaro, Deutsch-Ostafrikas, 1905-1906, Hemiptera, p. 138.

Type species *Mesohomotoma camphorae* Kuwayama, 1907 (original designation).

Head large, deeply cleft anteriorly, narrower than mesonotum. Vertex horizontal, somewhat raised above eyes laterally, with deep oblique sulcus from near base to anterior margin each side of medial suture, produced as small overhanging teeth at anterolateral angle. Genae contiguous, completely covering frons except for small portion around median ocellus, with small blunt lobes at posteroventral margin next clypeus. Median ocellus on dorsal side of head. Eyes small, rounded. Postocular portion of occiput well developed. Antennae long, over twice as long as width of head. Thorax quite flat dorsally. Pronotum very long, broad, flat, with pair of small angular processes on anterior margin, extending below margin laterally. Metanotum with pair of small sharp dorsal processes. Forewing large, long, membranous; basal vein very short; media and cubitus with common petiole; no pterostigma present, R_1 straight to costa; *Rs* very short, curved to costa; medial cell very large, not including apex of wing, cubital cell broad, much smaller than medial; distinct crossvein

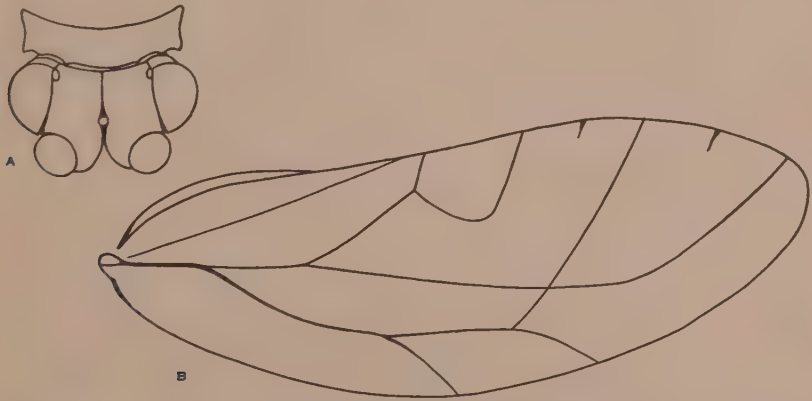

Fig. 18.—*Mesohomotoma* Kuwayama. *A,* head and pronotum; *B,* forewing. (Based on *M. hibisci* (Froggatt).)

between furcation of media and *Rs*. Metacoxa long, with well-developed meracanthus. Metatibia with basal spur and several large black apical spines. Proximal segment of metatarsus with 1 black claw.

The species described by Froggatt in 1901 as *Tyora hibisci* (type in Froggatt's collection) was made the type of the genus *Udamostigma* by Enderlein in 1910. Crawford (1920, p. 356; 1925, p. 32) placed *Udamostigma* in synonymy with the earlier *Mesohomotoma* Kuwayama. We can add no information as to its relationships. It occurs through much of the Pacific on *Hibiscus tiliaceus* Linn.

Genus PROTYORA Kieffer

Fig. 19

Protyora Kieffer, 1906, Z. wiss. InsektBiol. 2: 390.

Type species *Protyora sterculiae* (Froggatt), 1901 (= *Tyora sterculiae* Froggatt) (original designation Kieffer 1906).

Head deeply cleft anteriorly, narrower than mesonotum. Vertex horizontal, raised above level of eyes, with deep sulcate discal impressions, distinctly margined anteriorly. Median ocellus anterior, below margin of vertex. Genae not at all produced, contiguous, covering frons. Eyes small, rounded. Postocular portion of occiput large. Antennae very long, over 3 times as long as width of head, large basally, tapering. Thorax narrow, strongly arched. Pronotum large, long, strongly curved, strongly arched, extending far down laterally. Propleura large. Metanotum large, with 2 small dorsal protuberances. Forewing very long, bluntly angulate, membranous; basal vein very short, somewhat sinuate; media and cubitus with common petiole, long; R_1 parallel to costa nearly one-third of wing, forming large, open, scarcely thickened pterostigma; *Rs* short, turned to costa; medial cell not including apex of wing, larger than cubital; distinct crossvein from furcation of media to *Rs*. Legs long, slender. Tarsi very long. Metacoxa with meracanthus. Metatibia with basal spur, several black, apical spines. Proximal segment of metatarsus with 1 black claw.

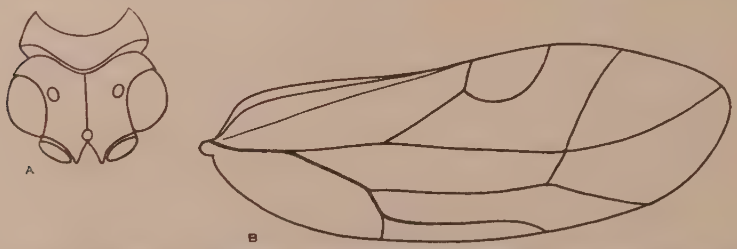

Fig. 19.—*Protyora* Kieffer. *A*, head and pronotum; *B*, forewing. (Based on *P. sterculiae* (Froggatt).)

Kieffer established *Protyora* for *Tyora sterculiae*, removing it from *Tyora* because of the open pterostigma ("da der Radius nicht gebalt ist"). Crawford in 1925, and again in 1927, suggested that *T. sterculiae* probably belonged in *Neocarsidara*, apparently overlooking Kieffer's genus. (So far as we can determine *Neocarsidara* is a nomen nudum as we are unable to find any other use of the name.) Froggatt's type of *T. sterculiae* is in his collection.

Genus TRIOZA Förster

Fig. 20

Trioza Förster, 1848, Verh. naturh. Ver. preuss. Rheinl. 5: 67.

Type species *Trioza urticae* (Linn.) (= Chermes urticae Linn.) (original designation Förster 1848).

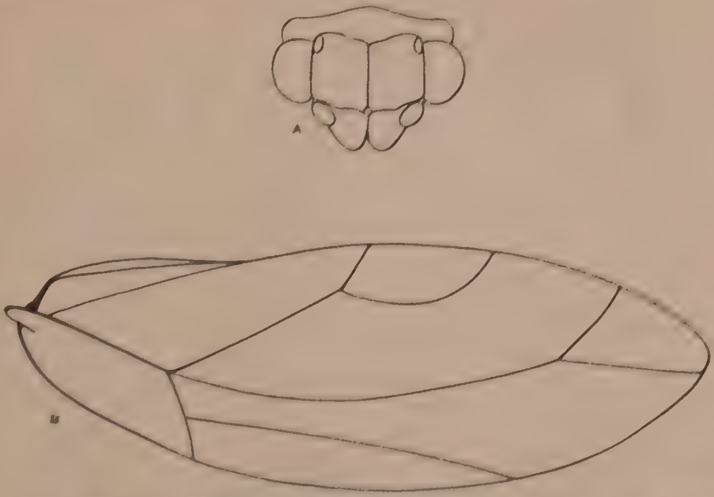

Fig. 20.- *Trioza* Förster. *A*, head and pronotum; *B*, forewing. (Based on undescribed species.)

Of the species placed in *Trioza* by Froggatt we find only *T. oleariae*, *T. eugeniae*, *T. tasmaniensis*, and *T. tristaniae* referable to that genus. The others differ so distinctly that we are placing them in two new genera. Froggatt's collection contains the types only of *T. eugeniae*, but it includes specimens named by him of the other three species listed here.

Genus SCHEDOTRIOZA, gen. nov.

Fig. 21

Type species *Schedotrioza eucalypti* (Froggatt), 1901 (= *Trioza eucalypti* Froggatt) (here designated).

Head large, narrower than mesonotum. Vertex with spare to abundant long pubescence, short, strongly depressed medially, raised laterally above level of eyes, strongly produced anteriorly each side of medial suture as prominent, overhanging lobes, incurved, touching, or nearly so, at apex. Genae produced as more or less conical, blunt, divergent processes. Median ocellus large, sunken between genae and overhanging lobes of vertex. Eyes rounded. Antennae long, usually twice as long as width of head or longer. Thorax well arched. Pronotum broad, moderately long, more or less produced dorsocaudally. Forewing large, somewhat angulate apically; basal vein long, trifurcate, no pterostigma; *Rs* long, somewhat sinuate; marginal cells large, about equal size. Legs stout. Metacoxa with meracanthus. Metatibia with small basal serration (or none), flared apically, armed with large, stout spines, 1 outer and 3 inner. Proximal segment of metatarsus without claws.

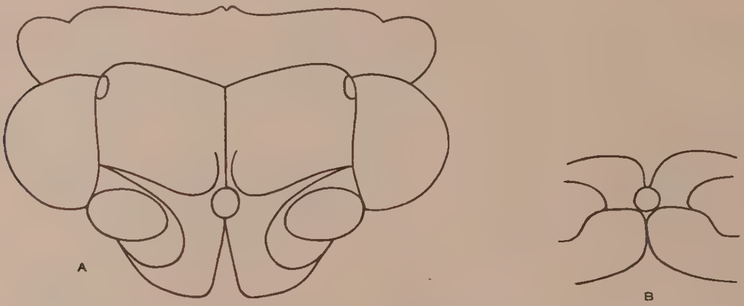

Fig. 21.—*Schedotrioza,* gen. nov. *A,* head and pronotum; *B,* head from ventral aspect. (Based on undescribed species.)

The very peculiar development of the vertex is in our opinion quite sufficient basis for separation of the species placed here from *Trioza.* In addition to the type species we assign *T. circularis* Froggatt, *T. orbiculata* Froggatt, and *T. carnosa* Froggatt to *Schedotrioza.* Type specimens of all four species are in Froggatt's collection.

The name *Schedotrioza* is derived from the Greek σχεδον (= nearly or almost) + *Trioza.*

Genus AACANTHOCNEMA, gen. nov.

Fig. 22

Type species *Aacanthocnema casuarinae* (Froggatt), 1901 (= *Trioza casuarinae* Froggatt) (here designated).

Head large, broader than mesonotum. Vertex long, broad, with anterior margin sharp, overhanging genal processes. Genal processes long, conical, narrowly rounded apically. Antennae moderate in length, longer than width of head. Eyes rounded. Postocular area of occiput large. Thorax rather flat dorsally, weakly arched anteriorly. Pronotum long, broad, with marked anteromedial projection. Forewing elongate, narrow, narrowly rounded apically; pterostigma absent; *Rs* short, curved to costa;

marginal cells equal. Legs stout. Metacoxa with small pointed meracanthus. Metatibia with basal spur, without apical spines. Proximal segment of metatarsus without claws.

The principal characters which serve to distinguish this genus from *Trioza* are the sharp overhanging anterior margin of the vertex and the complete lack of spines at the apex of the metatibiae.

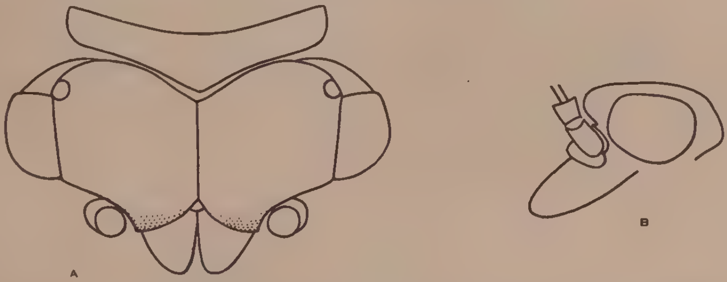

Fig. 22.—*Aacanthocnema*, gen. nov. *A*, head and pronotum; *B*, lateral aspect of head. (Based on *A. casuarinae* (Froggatt).)

T. dobsoni and probably *T. banksiae* are congeneric although the specimens of the latter species are in such poor condition that its exact structure cannot be determined. Froggatt's types of all three species placed here are in his collection.

The name *Aacanthocnema* is derived from the Greek negative prefix *a* + ακανθα (= spine) + κνημη (= tibia), in reference to the absence of apical spines on the metatibia.

OF DOUBTFUL POSITION

Genus PHYLLOLYMA Scott

Phyllolyma Scott, 1882, Trans. Ent. Soc. Lond. 1882: 456.

Type species *Phyllolyma fracticosta* (Walker), 1858*b* (= *Psylla fracticosta* Walker) (original designation Scott 1882).

From Scott's description and figures of Walker's material it is evident that *Phyllolyma* is related to *Thea* and *Cometopsylla* but it would seem to differ in the characters of the eyes and forewing. We are unable to establish its correct position without examining the type. Walker's specimens were from Tasmania.

OTHER SPECIES

The specimens of *Aphalara leptospermi* Froggatt (specimens named by Froggatt in his collection—location of type not known) are in such a poor state of preservation that we are unable to determine its proper position. It is perhaps generically distinct but we feel any disposition of it should await the collection of adequate material.

Psylla lidgetti Maskell (1898) from Victoria, *Trioza multitudinea* (Tepper) (Maskell 1898), *Aphalara tecta* Maskell (1898) from Victoria, *Psylla luteola* Erichson (1842), and *Psylla subfasciata* Erichson (1842), both from Tasmania, are at present unknown to us.

ACKNOWLEDGMENTS

The authors are grateful to the Entomology Branch, New South Wales Department of Agriculture, in particular Mr. E. H. Zeck and Mr. C. E. Chadwick, for assistance in checking certain of the late Mr. W. W. Froggatt's specimens in the Department's collection. The figures were prepared and arranged by Mr. L. A. Marshall of the Division of Entomology, C.S.I.R.O., from line drawings by the junior author. His help is gratefully acknowledged.

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LIST OF AUSTRALIAN SPECIES OF THE FAMILY PSYLLIDAE

Genus under which species is described is in parentheses, present disposition at right

		Page
acaciae-baileyanae Frogg. (*Psylla*)	*Psylla* Geoff.	247
acaciae-dealbatae Frogg. (*Psylla*)	*Psylla* Geoff.	247
acaciae-decurrentes Frogg. (*Psylla*)	*Psylla* Geoff.	247
acaciae-juniperinae Frogg. (*Psylla*)	*Psylla* Geoff.	247
acaciae-pendulae Frogg. (*Psylla*)	*Psylla* Geoff.	247
acaciae-pycnanthae Frogg. (*Psylla*)	*Psylla* Geoff.	247
alba Frogg. (*Pennapsylla*)	*Cardiaspina* Crawf.	236
artifex Schwarz. (*Cardiaspis*)	*Cardiaspina* Crawf.	235
assimilis Frogg. (*Rhinocola*)	*Eucalyptolyma* Frogg.	232
banksiae Frogg. (*Trioza*)	*Aacanthocnema*, gen. nov.	253
brunnea Frogg. (*Dasypsylla*)	*Dasypsylla* Frogg.	240
brunneus Frogg. (*Cardiaspis*)	*Cardiaspina* Crawf.	236
bullata Frogg. (*Lasiopsylla*)	*Lasiopsylla* Frogg.	235
candida Frogg. (*Psylla*)	*Psylla* Geoff.	247
capparis Frogg. (*Psylla*)	*Psylla* Geoff.	247
carinata Frogg. (*Aphalara*)	*Australopsylla*, gen. nov.	237
carnosa Frogg. (*Trioza*)	*Schedotrioza*, gen. nov.	252
casuarinae Frogg. (*Trioza*)	*Aacanthocnema*, gen. nov.	252
circularis Frogg. (*Trioza*)	*Schedotrioza*, gen. nov.	252
corniculata Frogg. (*Rhinocola*)	*Creiis* Scott	233
costatus Frogg. (*Rhinocola*)	*Creiis* Scott	233
dobsoni Frogg. (*Trioza*)	*Aacanthocnema*, gen. nov.	253
erratica Frogg. (*Eucalyptolyma*)	*Eucalyptolyma* Frogg.	232
eucalypti Maskell (*Rhinocola*)	*Ctenarytaina* F. & K.	244
eucalypti Frogg. (*Trioza*)	*Schedotrioza*, gen. nov.	251
eucalypti Dobson (*Psylla*)	*Spondyliaspis* Sig.	230
eugeniae Frogg. (*Trioza*)	*Trioza* Först.	251
falcatus Frogg. (*Lasiopsylla*)	*Lasiopsylla* (?) Frogg.	235
fici Tryon (*Psylla*)	*Mycopsylla* Frogg.	248
flavilabris Frogg. (*Aphalara*)	*Spondyliaspis* Sig.	231

LIST OF AUSTRALIAN SPECIES OF THE FAMILY PSYLLIDAE—*Continued*

		Page
formicosa Frogg. (*Thea*)	*Thea* Scott	238
[illegible] Walker (*Psylla*)	*Phyllolyma* Scott	[illegible]
frenchi Frogg. (*Psylla*)	*Psylla* Geoff.	247
[illegible] Frogg. (*Aphalara*)	*Eucalyptolyma* Frogg.	[illegible]
[illegible] Frogg. (*Aphalara*)	*Ctenarytaina* F. & K.	[illegible]
gracilis Frogg. (*Psylla*)	*Psylla* Geoff.	247
[illegible] Frogg. (*Spondyliaspis*)	*Spondyliaspis* Sig.	[illegible]
hibisci Frogg. (*Tyora*)	*Mesohomotoma* Kuw.	250
[illegible] Frogg. (*Spondyliaspis*)	*Spondyliaspis* Sig.	[illegible]
leai Frogg. (*Thea*)	*Thea* Scott	238
leptospermi Frogg. (*Aphalara*)	(?)	255
lidgetti Maskell (*Psylla*)	*Psylla* (?) Geoff.	254
[illegible] Frogg. (*Rhinocola*)	*Creiis* Scott	[illegible]
longipennis Walker (*Livia*)	*Creiis* Scott	238
luteola Erichson (*Psylla*)	*Psylla* (?) Geoff.	254
[illegible] Frogg. (*Syncarpiolyma*)	*Syncarpiolyma* Frogg.	[illegible]
[illegible] Frogg. (*Eucalyptolyma*)	*Eucalyptolyma* Frogg.	[illegible]
[illegible] Frogg. (*Spondyliaspis*)	*Spondyliaspis* Sig.	[illegible]
[illegible] Frogg. (*Rhinocola*)	[illegible], gen. nov.	[illegible]
mollis Frogg. (*Rhinocola*)	[illegible], gen. nov.	241
[illegible] Frogg. (*Rhinocola*)	*Eucalyptolyma* Frogg.	[illegible]
multitudinea Tepper (*Ascelis*)	*Trioza* (?) Först.	254
[illegible] Frogg. (*Rhinocola*)	[illegible], gen. nov.	[illegible]
[illegible] Frogg. (*Rhinocola*)	*Eucalyptolyma* Frogg.	[illegible]
[illegible] Frogg. (*Spondyliaspis*)	*Spondyliaspis* Sig.	[illegible]
[illegible] Frogg. (*Aphalara*)	*Ctenarytaina* F. & K.	[illegible]
[illegible] Sul. (*Spondyliaspis*)	*Spondyliaspis* Sig.	[illegible]
oleariae Frogg. (*Trioza*)	*Trioza* Först.	[illegible]
olivacea Frogg. (*Thea*)	*Thea* Scott	238
opaca Frogg. (*Thea*)	*Thea* Scott	238
[illegible] Frogg. (*Trioza*)	*Schedotrioza*, gen. nov.	[illegible]
[illegible] Frogg. (*Rhinocola*)	[illegible], gen. nov.	[illegible]
[illegible] Frogg. (*Lasiopsylla*)	*Creiis* Scott	[illegible]
[illegible] Frogg. (*Rhinocola*)	*Cardiaspina* Crawf.	[illegible]
[illegible] Frogg. (*Cardiaspis*)	[illegible], gen. nov.	[illegible]
[illegible] Frogg. (*Mycopsylla*)	*Mycopsylla* Frogg.	[illegible]
[illegible] Frogg. (*Rhinocola*)	[illegible], gen. nov.	[illegible]
[illegible] Frogg. ([illegible])	[illegible] Frogg.	[illegible]
[illegible] Frogg. (*Lasiopsylla*)	*Lasiopsylla* Frogg.	[illegible]
[illegible] Frogg. (*Cardiaspis*)	*Cardiaspina* Crawf.	[illegible]
[illegible] Frogg. (*Spondyliaspis*)	*Creiis* Scott	[illegible]
[illegible]*iegata* Kirkaldy (*Callistochermes*)	= *Dasypsylla brunnea* Frogg.	240
[illegible] Frogg. ([illegible])	[illegible] Frogg.	[illegible]
schizoneuroides Frogg. (*Psylla*)	*Psylla* Geoff.	247
[illegible] Frogg. (*Cardiaspis*)	*Cardiaspina* Crawf.	[illegible]
[illegible] Frogg. (*Psylla*)	[illegible], gen. nov.	[illegible]
[illegible] Frogg. (*Tyora*)	[illegible]	[illegible]
[illegible] Frogg. (*Lasiopsylla*)	*Lasiopsylla* (?) Frogg.	[illegible]
subfasciata Erichson (*Psylla*)	*Psylla* (?) Geoff.	254

LIST OF AUSTRALIAN SPECIES OF THE FAMILY PSYLLIDAE (*Continued*)

		Page
tasmaniensis Frogg. (*Trioza*)	*Trioza* Först.	251
tecta Maskell (*Aphalara*)	(?)	254
textrix Frogg. (*Cardiaspis*)	*Cardiaspina* Crawf.	236
tristaniae Frogg. (*Trioza*)	*Trioza* Först.	251
tryoni Frogg. (*Brachypsylla*)	*Brachypsylla* Frogg.	245
viridis Frogg. (*Rhinocola*)	*Creiis* Scott	233
viridis Frogg. (*Eriopsylla*)	*Eriopsylla* Frogg.	242
vittaformis Frogg. (*Cardiaspis*)	*Cardiaspina* Crawf.	236
wellingtoniae Frogg. (*Thea*)	*Thea* Scott	238

AUSTRALIAN HELORIDAE, INCLUDING MONOMACHIDAE (HYMENOPTERA)

By E. F. Riek*

(*Manuscript received June 23, 1954*)

Summary

The genera *Helorus*, *Monomachus*, *Ropronia*, *Vanhornia*, and *Tetraconus* are considered to belong in one family, the Heloridae, rather closely allied to the genus *Austroserphus* of the family Proctotrupidae. A new genus (with three new species) combining many of the characters of the above genera is described as well as a new species and a new subspecies of *Monomachus*.

Introduction

As originally established by Ashmead (1902) the Heloridae consisted of two subfamilies, the Monomachinae (*Monomachus* and *Ropronia*) and the Helorinae (*Helorus*). Crawford (1909) described the peculiar *Vanhornia* and erected a new family for it. Subsequent authors (e.g. Townes 1948) have considered these four genera in distinct families with *Tetraconus* Szépligeti 1903 a second genus in Monomachidae.

Undoubtedly they are all closely allied, differing slightly in wing venation and antennal segmentation and markedly so only in abdominal shape.

A new genus described below combines many of the characters of the known genera. It has the general habitus of *Ropronia*, the wing venation of *Monomachus*, and the antennal segmentation of *Helorus*. *Vanhornia* is the most distinct genus but this is mainly in abdominal shape, 13-segmented antenna, and head shape.

It is considered that the above five genera should be placed in the one family, Heloridae. Of the described genera only specimens of *Monomachus* have been examined.

It should be noted that the venation of the proctotrupid genus *Austroserphus* Dodd 1933 is very similar to that found in this family, particularly to *Ropronia* and *Vanhornia*, though the stem of *Rs* and the fused *Rs* + *M* are both incomplete in *Austroserphus*.

The family is characterized by 2-segmented trochanters; antennae inserted on the middle of the face; forewing with a stigma; mandibles dentate; antenna 13- to 15-segmented; tarsal claws simple or pectinate; and hindwing with or without distinct venation.

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KEY TO GENERA OF THE FAMILY HELORIDAE

1. Antenna with 15 segments 2
   Antenna with 13 or 14 segments 5
2. Tarsal claws pectinate; stem of *Rs* absent, fused *Rs* + *M* present; (abdomen not compressed, clubbed, petiole distinct) ....*Helorus* Latreille
   Tarsal claws simple; stem of *Rs* present, fused *Rs* + *M* absent 3
3. Abdomen long and thin, tapering; antennae inserted on a frontal protuberance ..4
   Abdomen laterally compressed, clubbed; antennae not inserted on a frontal protuberance (♀) ....*Austronia*, gen. nov.
4. Clypeus and cheeks without horns ....*Monomachus* Klug
   Clypeus with 2 horns and hind margin of cheek with a horn-like projection ....*Tetraconus* Szépligeti
5. Antenna with 14 segments 6
   Antenna with 13 segments; abdomen with only 2 (♀) or 4 (♂) visible tergites, the 1st covering most of the abdomen; stems of *Rs* and *M* and fused *Rs* + *M* present; mandible very short, with 3 large teeth, widely separated, and not meeting when closed ....*Vanhornia* Crawford
6. Abdomen strongly compressed; petiole distinct; stems of *Rs* and *M* and fused *Rs* + *M* present ....*Ropronia* Provancher
   Abdomen not compressed; fused *Rs* + *M* absent (♂) ....*Austronia*, gen. nov.

Genus HELORUS Latreille

Helorus Latreille, 1802, Hist. Nat. Crust. Ins. 3: 309.

Genotype *Helorus ater* Latreille, 1802, loc. cit. (monobasic).

Helorus is predominantly European but species are recorded also from North America, South America, and India. As far as is known *Helorus* is parasitic only on Chrysopidae (Neuroptera).

Genus ROPRONIA Provancher

Ropronia Provancher, 1886, Addit. Corr. Faune Ent. Canada, Hym.: 154.

Genotype *Ropronia pediculata* Provancher, 1886, loc. cit. (monobasic).

Nothing is known definitely of the biology of the species which are possibly limited to North America. One species is recorded doubtfully from China where it was possibly parasitic on *Periclista* (Tenthredinidae).

Genus VANHORNIA Crawford

Vanhornia Crawford, 1909, Proc. Ent. Soc. Wash. 11: 63.

Genotype *Vanhornia eucnemidarum* Crawford, 1909, loc. cit. (monobasic).

The single species is parasitic on eucnemid larvae in North America.

Genus TETRACONUS Szépligeti

Tetraconus Szépligeti, 1903, Ann. Hist. Nat. Mus. Hung. 1: 388.

Genotype *Tetraconus mocsaryi* Szépligeti, 1903, loc. cit. (monobasic).

The genus is recorded from South America.

Genus MONOMACHUS Klug

Monomachus Klug, 1841, Z. Entom. (Germar) 3(2): 378.

Genotype *Monomachus gladiator* Klug, 1841, loc. cit.

Body slender; abdomen long and thin, tapering; antenna with 15 segments; antennae inserted on a frontal protuberance; in the forewing stem of *Rs* present, fused *Rs* + *M* absent; clypeus and cheeks without horns.

The genus occurs in Australia and South America. Ashmead (1902) considered that the species may be parasitic on antlions. Specimens in the National Museum, Melbourne, are recorded as "? parasites of *Boreoides subulata* Hardy" (Diptera).

KEY TO THE AUSTRALIAN SPECIES OF THE GENUS MONOMACHUS

1. Head in lateral view with posteroventral angle rounded; lower margin of eye less than half vertical length of eye from lower margin of face. (Head without glabrous area behind ocelli; posterior region of pronotum with a single row of punctures across meson; petiole at base with fine rugae.) ....*australicus* Girault
   Head in lateral view with posteroventral angle pointed; lower margin of eye at least half vertical length of eye from lower margin of face 2
2. Glabrous area behind ocelli either broken at meson by scattered punctures or area entirely with scattered punctures 3
   Head with a median glabrous area behind ocelli, laterad with a few transverse sulci. (Posterior region of pronotum with an irregular zone of punctures across meson; petiole at base with limited (4-6), short, longitudinal carinae followed by an irregular, transversely rugose area.) ....*osmondi*, sp. nov.
3. Posterior region of pronotum with a single transverse row of strong setose punctures; petiole at base irregularly coarsely rugose ....*antipodalis bendora*, subsp. nov.
   Posterior region of pronotum with scattered punctures; petiole at base with limited, (4-6), short, longitudinal carinae, then irregularly finely rugose ....*antipodalis antipodalis* Westwood

MONOMACHUS ANTIPODALIS Westwood

Monomachus antipodalis Westwood, 1874, Thesaur. Entom. Oxon.: 126.
Monomachus antipodalis Schletterer, 1889, Berl. Ent. Z. 33: 225.

MONOMACHUS ANTIPODALIS ANTIPODALIS Westwood

Female

Body mostly black; legs, except coxae, red, but fore and hind femora somewhat darkened; antenna red but flagellum darkened at apex and scape and pedicel sometimes darkened; pronotum above, anteriorly, red and also red at posterolateral corners; thorax reddish discally at posterior scutum, and at parapside and axilla mesally; abdomen above pale on 3 and succeeding segments; more so 5 to apex; tegula red; mandible red except for teeth; lower margin of face (margining mandibles) narrowly red.

Head with glabrous area behind ocelli extending laterally towards the eye, but broken at meson by scattered punctures or with scattered punctures extending almost throughout; median projection from lower face (clypeus) usually distinctly trifid at apex; head in lateral view with the posteroventral angle pointed; lower margin of eye at least half the vertical length of eye from lower margin of face; posterior region of pronotum, except caudal margin more or less, with scattered punctures, the sunken area with distinct transverse sulci; axilla sparsely punctate mesally and posteromesally; scutellum glabrous but with widely scattered punctures extending towards the meson; propodeum with the median carina indistinct anteriorly; petiole at basal quarter irregularly, rather finely rugose, with limited (4-6) weak carinae at base; 1st funicle distinctly longer than scape, succeeding segments decreasing, apical club segment 2½ times as long as wide.

Type.—♀. Location not known.

Type locality.—Melbourne, Vic.

Specimens examined.—VICTORIA: Murrumbeena (16.v.1924, A. J. Campbell), 5 ♀♀, in National Museum, Melbourne, ? parasite on *Boroides subulata* Hardy; Mordialloc (May 1907), 1 ♀, in National Museum, Melbourne; Mordialloc (25.iv.1930, A. N. Burns), 2♀♀, in A. N. Burns Collection; Mordialloc (24.v.1933, A. N. Burns), 1♀, in A. N. Burns Collection; Carrum (19.v.1945, C. Oke), 3♀♀, in A. N. Burns Collection; Olinda (26.v.1940, F. E. Wilson), 1♀, in A. N. Burns Collection; Melbourne (Mar. 1929, Blackbourne), 1♀, in Queensland Department of Agriculture, Entomology Branch Collection.

The propodeum is variable in this species. The median carina is either present or absent depending on the ornamentation and its strength. The punctures of the posterior half of the pronotum also are variable.

MONOMACHUS ANTIPODALIS BENDORA, subsp. nov.

Plate 1, Figs. 1 and 2

Female

Body mostly black; legs, except coxae, all red; antenna all red; pronotum all dark; abdomen above pale on 2, less so on 4 and succeeding; tegula red; mandible red except for teeth; lower margin of face (margining mandibles) narrowly red.

Head with glabrous area behind the ocelli extending laterally towards the eye but broken at meson by scattered punctures; median projection from lower face distinctly trifid at apex; head in lateral view with the posteroventral angle pointed; lower margin of eye at least half the vertical length of eye from lower margin of face; posterior region of pronotum with a single transverse row of strong punctures, pronotum widely glabrous at meson except for this transverse row and 2 punctures in the sunken zone; axilla sparsely punctate, particularly mesally and posteromesally; scutellum glabrous but with scattered punctures towards meson; propodeum with distinct median carina, particularly anteriorly, the laterad glabrous area almost obsolete; petiole at basal quarter irregularly coarsely rugose; 1st funicle segment distinctly longer than scape.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Bendora, A.C.T. (21.iii.1951, E. F. Riek).

Only the holotype is known. The subspecies is distinguishable readily from the typical form on the ornamentation of the pronotum and of the petiole.

MONOMACHUS AUSTRALICUS Girault

Monomachus australicus Girault, 1925, some Gem-like or Marvellous Inhabitants of the Woodlands etc.: 2.

Female

Body mostly black; legs, except coxae, mostly red, but basal half of all femora and hind tibia above, except at base, dark; antenna red, but scape and pedicel darkened; pronotum pale above at caudal half except widely at meson, posterolateral corners pale; thorax pale at scutellum, except anteriorly and narrowly at scutum discally; abdomen above pale at apical third of petiole, segment 2 at meson, 3 and 4 except at apex, succeeding all pale; tegula red; mandible red except for teeth; head reddish narrowly at vertex, extending laterally and widening behind the eye, narrowly pale on mesal margin of eye over lower half, lower margin bordering mandibles narrowly red.

Head without a distinct glabrous area behind the ocelli, completely punctate; median projection from lower face apparently trifid at apex (partly obscured by glue); head in lateral view with the posteroventral angle rounded; lower margin of eye less than half the vertical length of eye from lower margin of face; posterior region of pronotum with a single transverse row of strong punctures; pronotum, behind the transverse carina at the anterior declivity, widely glabrous at meson except for a single large puncture in the sunken area; axilla sparsely punctate only mesally; scutellum glabrous except towards the lateral margins and there sparsely punctate; propodeum with the median carina indistinct anteriorly, laterad glabrous area very small and finely etched; petiole at basal quarter irregularly finely rugose, with a few coarser rugae at base, without a laterad carina at base; 1st funicle segment distinctly longer than scape.

Type.—Holotype ♀ in the Queensland Department of Agriculture, Entomology Branch Collection.

Type locality.—Cleveland, Qld. (14.v., A. A. Girault), on dead tree.

Only the holotype is known. The species has a most distinctive head, with rounded posteroventral angle, short face, and without a glabrous area behind the ocelli.

MONOMACHUS OSMONDI, sp. nov.

Female

Body mostly black; legs, except coxae, red, but all trochanters, darkened middle and hind femora darkened over part of base, but pale at apex; antenna all red; posterolateral corners of pronotum red; abdomen with segment 2 and less so petiole pale above; tegula red; mandible red except for teeth; lower margin of face (margining mandibles) narrowly red.

Head with a median glabrous area behind the ocelli, only as wide as the space between the ocelli, laterad with a few transverse sulci; median projection from lower face not distinctly trifid; head in lateral view with the posteroventral angle pointed; lower margin of eye at least half the vertical length of eye from lower margin of face; posterior region of pronotum with irregular punctures across the meson, forming a distinct zone, pronotum glabrous only narrowly at the sunken zone; axilla sparsely punctate particularly mesally and posteromesally; scutellum glabrous except towards the lateral margins and there sparsely punctate; propodeum with only a faint median carina, with a large glabrous area on each side laterad at about the middle of its length; petiole at base with limited (4-6) short carinae followed by an irregular transversely rugose area (which extends to base narrowly at meson); 1st funicle segment distinctly longer than scape.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Glen Osmond, S.A. (13.v.1937, D. Swan).

Only the holotype is known. The species is more closely allied to *antipodalis* than to *australicus*. It differs from the former principally in the ornamentation of the head and of the pronotum.

Genus AUSTRONIA, nov.

Genotype *Austronia nitida*, sp. nov.

Female

Habitus of *Ropronia* but differing in the structure of the antenna and in wing venation; abdomen shaped as in *Ropronia* but segment 2 (1st after petiole) quite small; pronotum quite large, upper surface almost half as long as wide, with the carina at the anterior declivity broken at the meson; venation of both wings basically as in *Monomachus*, forewing with the fused *Rs* + *M* vein obsolete and the *m-cu* crossvein meeting *CuA* well before the forking of *CuA*, hindwing with an additional vein to that seen in *Helorus* but with the basad vein similar; a transverse vein arising from *R* somewhat before its apex, reaching the hind margin and curved towards the base, sometimes with a basal stump at the point of greatest curvature; tarsal claws simple; antenna 15-segmented; ovipositor issuing before apex.

Male

Similar to female but antenna only 14-segmented and pronotum rather shorter.

Nothing is known of the biology of the species.

The three species can be separated readily on the colour of the thorax and legs.

AUSTRONIA NITIDA, sp. nov.

Plate 1, Fig. 4

Female

Shining black; legs red, except coxae and trochanters; tegula red; scape narrowly red at base; wings slightly infuscated, venation fuscous.

Scape stout, pedicel quadrate, 1st funicle longer than scape, succeeding segments decreasing regularly, 12th only slightly longer than wide, apical segment somewhat longer; head setose, finely so at vertex; dorsal thorax finely setose; propodeum with a median carina over basal half, irregularly, coarsely, longitudinally rugose over apical half, coarsely, transversely rugose at basal half; petiole finely, irregularly rugose; abdomen punctate and setose, less so at meson, segment 2 at meson twice as long as subequal succeeding segments, 7 visible segments.

Type.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Lake St. Clair, Tas. (25.i.1949, E. F. Riek). A 2nd ♀, Nichols Hut, Tas., 2500 ft (21.i.1949, N. B. Tindale) in the South Australian Museum, Adelaide.

AUSTRONIA RUBRITHORAX, sp. nov.

Plate 1, Fig. 3

Female

Head and abdomen shining black, thorax, except below, all red; legs, except coxae in part, all red; abdominal petiole all red; scape narrowly red at base; wings clear, venation fuscous.

Apical club segment shorter than in *nitida*, 12th funicle almost quadrate, apical segment not twice as long as wide; pronotum with carina at declivity distinctly broken laterally as well as at meson; propodeum more finely rugose than in *nitida*, with a median carina over basal half, surface mostly foveate and rugose; petiole with ornamentation similar to but finer than on propodeum.

Type.—Holotype ♀ and paratype ♀ ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra.

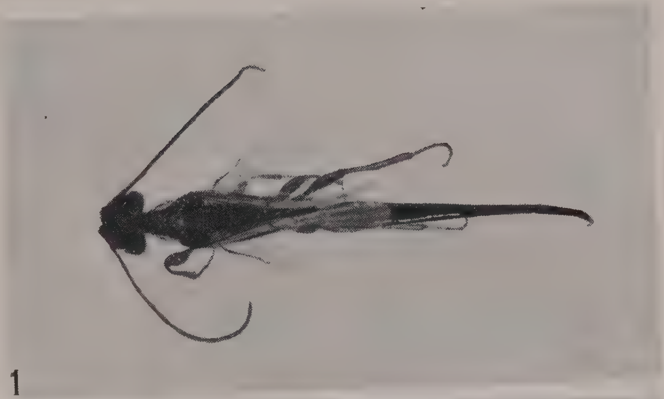
Type locality.—Beaconsfield, Vic. (15.xi.1946, B. B. Given).

Specimens examined.—NEW SOUTH WALES: Twenty miles east of Canberra (20.xi.1953, E. F. Riek), 4 ♀ ♀. The red thorax and abdominal petiole clearly distinguish this species from *nitida*.

AUSTRONIA NIGRICULA, sp. nov.

Male

Shining black; legs black or dark except for tarsi mostly and fore tibia; tegula black; wing somewhat infuscated, particularly at base and costal space.



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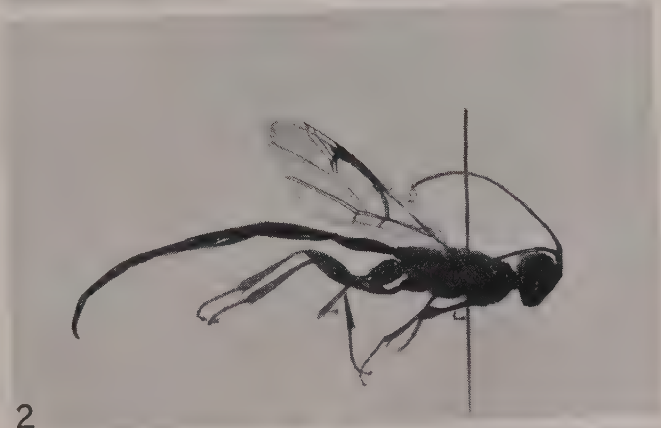

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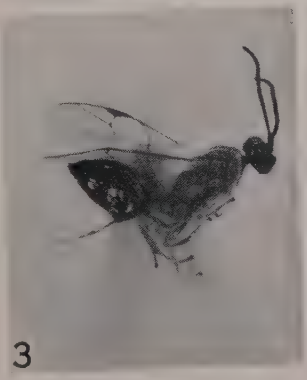

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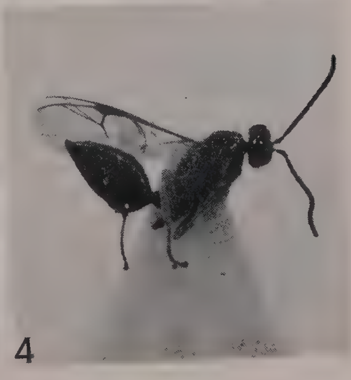

4

Antenna as in *nitida* but with only 14 segments, apical segment about twice as long as wide, penultimate distinctly longer than wide, pronotum not half as long as wide, carina at anterior declivity entire; dorsal thorax shining with numerous long setae; propodeum coarsely irregularly foveate, without distinct median carina; petiole almost glabrous at meson, irregularly longitudinally rugose laterally; abdomen mostly glabrous, with fine scattered setae laterally, extending to meson on apical segments, segment 2 (1st after petiole) the longest, segment 3 almost as long, succeeding segments decreasing, 6 visible segments as well as petiole.

Type.—Holotype ♀ in the Queensland Museum, Brisbane.

Type locality.—National Park, Qld. (25.x.1923, H. Hacker).

Only the holotype is known. It shows a general similarity to the male of *Ropronia* but has a distinct wing venation. This could possibly be the male of one of the other two species of which only the female is known.

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EXPLANATION OF PLATE 1

Fig. 1.—*Monomachus antipodalis bendora*, subsp. nov., holotype female, dorsal view. × *c.* 5.

Fig. 2.—*Monomachus antipodalis bendora*, subsp. nov., holotype female, lateral view. × *c.* 5.

Fig. 3.—*Austronia rubrithorax*, gen. et. sp. nov., holotype female. × *c.* 6.

Fig. 4.—*Austronia nitida*, gen. et sp. nov., holotype female. × *c.* 6.

REVISION OF THE AUSTRALIAN MAYFLIES (EPHEMEROPTERA)

I. SUBFAMILY SIPHLONURINAE

By E. F. RIEK[*]

(*Manuscript received November* 24, 1954)

Summary

The present paper deals with the systematics of the adults and nymphs of the Australian species of the subfamily Siphlonurinae. Two new species of *Mirawara* are described.

INTRODUCTION

This is the first of a series of papers dealing with the systematics of the Australian mayfly fauna. As many of the imagos and subimagos have not been associated with their nymphs the descriptions, in the first place, will be limited to the winged stages. An exception is made of the subfamily Siphlonurinae where the nymphs have been worked out. Subsequently it is hoped to record something of the biology and of the immature stages.

In this series of papers the order will be divided into subfamily groups. Part I deals with the subfamily Siphlonurinae, the largest and most handsome of our mayflies.

This subfamily is more or less restricted to the highlands, particularly to the south-eastern corner, and to Tasmania. Tillyard has recorded the species known to occur in Tasmania and in the Kosciusko region of New South Wales. Most records actually are from these two areas but *Mirawara,* which occurs at Kosciusko, ranges as far north as central Queensland.

There is a single recorded species from Tasmania and six from the Kosciusko area. In this paper another two species are added to the fauna, one of them occurring in the highlands of New South Wales and one in the highlands of coastal Queensland.

Subfamily **SIPHLONURINAE**

Adult

Large species, wings with numerous crossveins; cubital area of forewing with a number of more or less sinuous veins extending from the 1st branch of the cubitus to the wing margin; hindwing small but with numerous veins; 2, or sometimes 3, caudal filaments; hind tarsi with 4 free segments in most species; forceps base usually very long, its apical margin, between the forceps limbs, more or less deeply emarginate; forceps more or less distinctly 4-segmented, basal segment short, usually rather ring-like, often more or less fused with the 2nd segment, which is often

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strongly bowed, 2, rarely 3, terminal segments, which together are not longer than the 2nd segment; penes variable; subanal plate of female variable.

Nymph

Body more or less cylindrical, head horizontal or nearly so; hind corners of the abdominal segments produced backwards to form tooth-like projections; lateral caudal filaments ciliated on the inner border only. The rather large nymphs are to be found on the surface of rock in swift flowing water but also in the quieter waters of stream pools and lakes. In some cases the nymphs can be observed under the spray of falls out of the water. Nymphs normally with 7 pairs of abdominal gills, quite conspicuous and usually standing away from the body. There are only 4 pairs in *Tasmanophlebia*.

Key to the Australian Genera of the Subfamily Siphlonurinae

1. In the forewing MP_2 is attached basally to CuA; in the hindwing triad on MP arises close to the base; tarsal claws alike, both sharp; 3 well-developed tail-filaments in each sex ....*Ameletoides* Tillyard

   In the forewing MP_2 is normal, not attached to CuA; in the hindwing triad on MP varies; tarsal claws dissimilar, 1 sharp and 1 blunt; appendix dorsalis obsolescent or entirely absent 2

2. Hind tarsus appearing 5-segmented, the line of suture between metatarsus and tibia preserved; in the hindwing triad on MP small; in the forewing CuP and $1A$ at their bases converge before continuing parallel ....*Coloburiscoides* Lestage

   Hind tarsus only 4-segmented, metatarsus fused to tibia 3

3. In the hindwing MP forks close to the base but no distinct triad is developed; in the forewing CuP and $1A$ are more or less parallel for their whole length; male claspers 4-segmented ....*Mirawara* Harker

   In the hindwing triad on MP only over the apical half or less of the vein; in the forewing CuP and $1A$ at their bases converge before continuing parallel; male claspers 3-segmented ....*Tasmanophlebia* Tillyard

Genus AMELETOIDES Tillyard

Ameletoides Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 6.

Genotype *Ameletoides lacus-albinae* Tillyard, 1933, loc. cit. (original designation).

Adult

Forewing with tornus at about two-fifths of wing-length; MP_2 is secondarily attached to CuA; bullae present; hindwing distinctly less than half as long as forewing, its costa only slightly angulated near base; fore legs on the male imago longer than the body, about as long as the forewing; those of the female imago shorter than the body; tarsal claws of all legs similar, both sharply pointed, smooth; tarsus with 1st segment shorter than that of the 2nd; the hind tarsus about equal in length to the hind tibia; 3 tail-filaments present, the appendix dorsalis almost as long as the cerci.

Nymph

Free-swimming, rather shrimp-like, somewhat laterally flattened, and with thorax slightly humped; head small, hypognathous, the eyes lateral, the antennae short; mandibles with a single large incisor; maxillary and labial palpi, 3-segmented; abdomen tapering posteriorly; 7 pairs of gills, 1 pair to each of segments 1-7; gills simple, lamellate, consisting of an oval portion, supported by a sclerotized rim and an unsupported dorsal flange; tail-filaments short, about half as long as body.

AMELETOIDES LACUS-ALBINAE Tillyard

Ameletoides lacus-albinae Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 6.
Ameletoides lacus-albinae Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Ameletoides lacus-albinae Harker, 1954, *Trans. R. Ent. Soc. Lond.* 105: 266.

Tillyard described this species, the only one of the genus, in detail from male and female imagos and subimagos and nymphs.

Types.—Holotype ♂ imago, allotype ♀ imago, type ♂ subimago, type ♀ subimago all taken at Lake Albina, Mt. Kosciusko, 6350 ft. Type nymph and nymphal exuviae taken on rocks in the lake. Types in the Tillyard Collection, British Museum; types missing (see Harker 1954). Paratypes of both imagos and subimagos in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Lake Albina, Mt. Kosciusko, N.S.W., 6350 ft.

Distribution.—NEW SOUTH WALES: Kosciusko area: Lake Albina (Feb. 1929 and 1930, R. J. Tillyard); The Chalet, Mt. Kosciusko (9.ii.1946, E. F. Riek).

Genus TASMANOPHLEBIA Tillyard

Tasmanophlebia Tillyard, 1921, Proc. Linn. Soc. N.S.W. 46: 410.
Tasmanophlebia Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 350.
Tasmanophlebioides Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 350.

Genotype *Tasmanophlebia lacustris* Tillyard, 1921, loc. cit. (original designation).

Adult

Forewing with tornus at one-half the wing-length or even somewhat beyond; triad of *MP* normal, arising very close to the origin of that vein; bullae faintly indicated or absent; hindwing about half as long as forewing, or somewhat more, and very nearly as wide, the humeral angle well developed, obtuse; triad of *MP* very small, distally placed; fore legs of the male imago nearly as long as forewing; those of female imago only half as long as forewing, or less; tarsi of all legs, except fore legs of male, only 4-segmented, the basal segment being more or less fused with the tibia; this fused 1st segment about as long as the tibia, and longer than any of the other segments; tarsal claws of all legs strongly dissimilar, 1 sharply hooked and 1 broad and blunt, with rounded apex; abdomen narrowly cylindrical, tapering posteriorly, without lateral dilatations on any of the segments; only 2 tail-filaments present, the cerci longer than the abdomen, the appendix dorsalis reduced to a minute remnant.

Nymph

Free-swimming, dorsoventrally flattened, the thorax not humped; abdominal segments with median dorsal crest and lateral flanges having strongly projecting posterior angles; head small, hypognathous, with laterally placed eyes and short antennae; mandibles with 2 sharp incisors; maxillary and labial palpi 3-segmented; hypopharynx bilobed; abdomen tapering posteriorly; only 4 pairs of gills, carried dorsally upon the abdomen, 1 pair on each of segments 1-4, the 1st a pair of strongly sclerotized lamellae forming an operculum to the other 3, which fit under it owing to the shortening of the 1st 4 abdominal segments; tail-filaments somewhat more than half as long as the abdomen, the appendix dorsalis somewhat shorter and much less strongly built than the cerci.

This genus appears to be well represented in the lakes and streams at high altitudes, both on the Australian mainland and in Tasmania. It is fairly closely related to the New Zealand genus *Oniscigaster* McLachlan, from which it can be distinguished in the adult by the narrow, cylindrical abdomen without any lateral dilatations of the segments, by the generally smaller size, and in the nymph by the peculiar specialization of the gills.

Lestage (1935) separated the two Australian species generically from the Tasmanian species. He based the division mainly on the forking of *MP* in the hindwing and on the structure of the male genital forceps. Lestage considered the forceps of *lacustris* to be 4-segmented whereas they are really only 3-segmented as in *lacus-coerulei* and *nigrescens*. The forking of *MP* in the hindwing varies with the individual specimen in all three species, in *lacustris* it may fork closer to the wing margin than figured by Tillyard, and in *lacus-coerulei* and *nigrescens* it may be more basad but it is always well after the middle of the vein.

KEY TO THE SPECIES OF THE GENUS TASMANOPHLEBIA

Imagos

1. Species of larger size, forewing 13-16 mm; wing membrane slightly clouded, darkened along the costal area, with brownish hues ......*lacus-coerulei* Tillyard
   Species of smaller size, forewing 10-12 mm; wing membrane clear in part, the costal area of forewing darker over the apical half, blackish 2
2. In male, hindwing darkened over anterior third, forewing with the basal one-quarter darkened ....*lacustris* Tillyard
   In male, hindwing with the darkening more limited to the basal half of the costal area, forewing darkened only over the anal vein ....*nigrescens* Tillyard

Subimagos

1. Wings distinctly bicolorous; the costal area and apex widely of forewing, and margins of hindwing, dark grey, remainder of wing lighter grey ....*lacus-coerulei* Tillyard
   Wings nearly unicolorous but with the same pattern as above ....*lacustris* Tillyard and *nigrescens* Tillyard
   (*nigrescens* is a little smaller and darker than *lacustris*)

TASMANOPHLEBIA LACUSTRIS Tillyard

Tasmanophlebia lacustris Tillyard, 1921, Proc. Linn. Soc. N.S.W. 46: 410.
Tasmanophlebia lacustris Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 350.
Tasmanophlebia lacustris Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Tasmanophlebia lacustris Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 267.

The species was described by Tillyard from male and female imagos and subimagos. The nymph is unknown.

Types.—Holotype ♂ imago and allotype ♀ imago reared from subimagos. Also ♂ and ♀ subimagos taken at the same time as the imaginal types. Types in the Tillyard Collection, British Museum. There is a long series of paratypes from Lake Echo in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Lake Lilla near Cradle Mt., north-west Tasmania, 3200 ft.

Distribution.—TASMANIA: Lake Lilla and Lake Echo (27.i.1933, R. J. Tillyard); Lake St. Clair (25.i.1949, E. F. Riek); Lake Dobson (22.i.1949, E. F. Riek).

There is some variation in the shape of the claspers in the males from the various localities but insufficient material is available to evaluate this character. The colouring at the base of the wing also varies considerably.

TASMANOPHLEBIA LACUS-COERULEI Tillyard

Tasmanophlebia lacus-coerulei Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 18.
Tasmanophlebioides lacus-coerulei Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 350.
Tasmanophlebia lacus-coerulei Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Tasmanophlebiodes lacus-coerulei Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 267.

Tillyard described the species in detail from all stages.

Types.—Holotype ♂ imago, allotype ♀ imago, type ♀ subimago, and type ♂ subimago taken at Blue Lake, Mt. Kosciusko, 6200 ft. Type nymph and nymphal exuviae taken on rocks in lake. Types in Tillyard Collection, British Museum. There is a long series of paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Blue Lake, Mt. Kosciusko, N.S.W., 6200 ft.

Distribution.—So far, this species has only been found in the Blue Lake, where the nymph may be seen resting on large rocks and boulders which occur in it, or sometimes on the pebbly bottom.

TASMANOPHLEBIA NIGRESCENS Tillyard

Tasmanophlebia nigrescens Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 18.
Tasmanophlebioides nigrescens Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 350.
Tasmanophlebia nigrescens Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Tasmanophlebiodes nigrescens Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 267.

Tillyard described the species in detail from all stages.

Types.—Holotype ♂ imago, allotype ♀ imago, type ♂ subimago, and type ♀ subimago taken at Spencer's Creek, Mt. Kosciusko, 5700 ft. Type nymph and nymphal exuviae taken at the same locality. Types in the Tillyard Collection, British Museum. There is a long series of paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Spencer's Creek, Mt. Kosciusko, N.S.W., 5700 ft.

Distribution.—NEW SOUTH WALES: The species has also been taken at "The Lake", Mt. Kosciusko (31.xii.1932, R. J. Tillyard, 5000 ft, and at Rule's Point, upper Murrumbidgee River (20.xii.1934, R. J. Tillyard), 4450 ft.

This species comes fairly close to the genotype *lacustris* from Tasmania. It is about the same size or a little smaller. The male genitalia of the imagos differ very slightly as do the veins of the hindwings. The wings of the male imago in the type species are the more heavily pigmented. The form *nigrescens* may yet be considered a subspecies of *lacustris*.

COLOBURISCOIDES Lestage

Coloburiscus Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 29.
Coloburiscoides Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 354.

Genotype *Coloburiscus giganteus* Tillyard, 1933, loc. cit. (original designation).

Adult

Forewing with tornus at about two-fifths of wing-length from base; triad of *MP* arising close to the origin of that vein, with MP_2 much curved near its origin and approaching very close to *CuA* below it; hindwing less than half as long as forewing, the humeral angle strongly developed; triad of *MP* small, distally placed; fore legs of male imago from two-thirds to nearly as long as the forewing; those of the female much shorter; tarsi of all legs appearing 5-segmented, the line of suture between the metatarsus and tibia preserved, shorter than the tibiae; tarsal claws of each leg strongly dissimilar, 1 sharply hooked and 1 blunt; those of fore legs of male sometimes hypertrophied; abdomen tapering posteriorly, the 1st segment closely connected with the thorax; posterolateral angles of 9th tergite produced into spines; only 2 tail-filaments present, the cerci longer than the abdomen, the appendix dorsalis reduced to a mere remnant.

Nymph

Sedentary type, clinging to rocks in rapid waters; body somewhat S-shaped in lateral view, the thorax huge and strongly humped, the abdomen somewhat flattened dorsoventrally, but without a dorsal crest; head of medium size, hypognathous, with fairly large eyes, laterally placed, and antennae somewhat longer than the head; mandibles with 2 distinct incisors, strongly projecting molar area, and a large brush of long hairs on the upper surface; maxillary and labial palpi 2-segmented, large; labrum, maxillae, and labium very hairy, hypopharynx entire; legs rather short, spiny, the fore and middle femora also provided with long hairs; tarsal claws simple; gills carried upright dorsally upon the abdomen, 1 pair on each of segments 1-7 inclusive; each gill is deeply bifid and strongly spinose; tail-filaments 3, the cerci well developed, the appendix dorsalis variable.

Species of this genus occur in south-eastern Australia, mainly in the highlands but also in the coastal streams around Melbourne. There are three species, the two from Mt. Kosciusko being very large. They occur only where the flow of water is permanent and where there are rocky rapids suitable for the nymphs. The third species prefers the lower country and is known from near Melbourne and close to Canberra. The genus is closely allied to the New Zealand *Coloburiscus*.

Key to the Species of the Genus Coloburiscoides

Imagos

1. Costal and subcostal spaces of the forewing entirely light reddish brown .... *giganteus* (Tillyard)

   Costal and subcostal spaces of the forewing in the pterostigmatic region greenish grey, otherwise clear .... *munionga* (Tillyard)

   Costal and subcostal spaces of the forewing in the pterostigmatic region pale brown, otherwise clear .... *haleuticus* (Eaton)

Subimagos

1. Forewing, except for costal and subcostal spaces uniformly coloured 2

   Forewing patterned in grey and water white with a large transverse area at the furcation of *MA* .... *munionga* (Tillyard)

2. Wings uniformly very pale grey .... *haleuticus* (Eaton)

   Forewing dark grey, tending to black, hindwing lighter in colour, costal and subcostal spaces semiopaque black .... *giganteus* (Tillyard)

The species *haleuticus,* which combines many of the characters of the other two species, is generally considerably smaller than them. The subimago has the more or less uniform pigmentation of *giganteus* but the imago has the major portions of the costal and subcostal spaces clear as in *munionga.*

COLOBURISCOIDES MUNIONGA (Tillyard)

Coloburiscus munionga Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 29.
Coloburiscoides munionga Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 354.
Coloburiscus munionga Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Coloburiscoides munionga Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 266.

The species was described fully from all stages by Tillyard.

Types.—In the Tillyard Collection, British Museum. Types missing (see Harker 1954). Paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Mt. Kosciusko, N.S.W.

Distribution.—NEW SOUTH WALES: Digger's Creek, Spencer's Creek, and Perisher Creek, Mt. Kosciusko (Jan. 1929 and Dec. 1931, R. J. Tillyard).

The species can be distinguished readily from *giganteus* by its smaller size, by lack of the darkened costal and subcostal spaces of the forewing in the imago, and more especially by the strongly mottled wings of the subimago.

COLOBURISCOIDES GIGANTEUS (Tillyard)

Coloburiscus giganteus Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 22.
Coloburiscoides giganteus Lestage, 1935, Bull. (Ann.) Soc. Ent. Belg. 75: 354.
Coloburiscus giganticus Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Coloburiscoides giganteus Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 266.

This species was described fully from all stages by Tillyard.

Types.—Holotype ♂ imago, allotype ♀ imago, and type ♂ and ♀ subimagos all taken on Digger's Creek, Mt. Kosciusko, 5000 ft. Type nymph and nymphal exuviae taken under rocks in the same locality. Types in the Tillyard Collection, British Museum; types missing (see Harker 1954). A series of paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Digger's Creek, Mt. Koscuisko, N.S.W., 5000 ft.

Distribution.—This mayfly has only been taken towards the end of January or beginning of February on Digger's Creek and other similar, rapid, rocky creeks on Mt. Kosciusko. The nymphs cluster in small colonies under rocks in the swiftest parts of the stream.

COLOBURISCOIDES HALEUTICUS (Eaton)

Coloburus haleuticus Eaton, 1871, Trans. Ent. Soc. Lond. 1871: 133.
Coloburiscus haleuticus Tillyard, 1933, Proc. Linn. Soc. N.S.W. 58: 22.
Coloburiscus haleuticus Harker, 1950, Proc. Linn. Soc. N.S.W. 75: 29.
Coloburiscus haleuticus Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 266.

Male Imago

Dried. Forewing 15.5 mm; length of body 15 mm; cerci 18 mm; appendix dorsalis 0.5 mm.

Colouring much as in *munionga* except that all parts are paler. Differs in the colour of the claspers, which are dark except for the basal half of the 1st segment; cerci dark to base, 1st segment not paler; forewing hyaline except at extreme base and for the pale brown costal and subcostal spaces particularly in the pterostigmatic region; terminalia as in *munionga* but the ventral of the 3 processes of the penis shorter and more rapidly tapered to the strongly incurved apex (in *munionga* the apex is directed ventrally and is evenly tapered to a point); posterolateral margin of the 9th abdominal segment rather bluntly produced, not half as long as the 10th segment, 8th segment virtually not produced.

Type.—Holotype ♂ in the National Museum, Melbourne.

Type locality.—Unknown.

Distribution.—In the National Museum there are another 2 specimens, 1 ♂ from near Melbourne and 1 ♀ subimago from Heidelberg, Vic. 1 ♀

from Jeeralong, Vic. (8.xi.1949, A. N. Burns), in the Burns Collection. The species occurs also near Canberra and on the upper reaches of the Murrumbidgee. AUSTRALIAN CAPITAL TERRITORY: Coree Creek (28.xi.1930, A. L. Tonnoir), 1 ♂, bred from nymph. Upper Cotter River (above dam) (13.xi.1948, E. F. Riek), 1 ♂ subimago; same locality (7.iii.1948, E. F. Riek), 1 ♀ subimago. NEW SOUTH WALES: Bolairo (11.iii.1951, E. F. Riek), 1 ♀ subimago.

This species differs from *munionga* in the colour of the wings of both subimago and imago, in the colour of the claspers and cerci of the male, and also in the shape of the 8th and 9th abdominal segments and in the male terminalia.

Genus MIRAWARA Harker

Mirawara Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 261.

Genotype *Mirawara aapta* Harker, loc. cit. (original designation).

Adult

Forewing with tornus at about two-fifths of wing-length; triad of *MP* arising close to the origin of that vein; bullae reduced; hindwing distinctly less than half as long as fore, its costa only slightly angulated near base; *MP* forked close to its base but no triad developed till near the wing margin; fore legs of male imago nearly as long as the forewing; those of the female much shorter; tarsi of all legs only 4-segmented, the basal segment more or less fused with the tibia; this fused 1st segment shorter than the tibia, but as long as or longer than any of the other tarsal segments; tarsal claws of all legs strongly dissimilar, 1 sharply hooked and 1 broad, obliquely truncate at apex; abdomen tapering posteriorly, the 1st segment closely connected with the thorax; posterolateral angles of 9th tergite produced into spines; only 2 tail-filaments, the cerci, which are longer than the abdomen; tergite of the 10th somite produced posteriorly over the minute appendix dorsalis; male claspers distinctly 4-segmented, with 1 large basal segment and 3 small apical segments.

Nymph

Shrimp-like, actively swimming type, resting on rocks in quiet water or clinging to the under surface in more rapidly flowing water; body somewhat S-shaped in lateral view; thorax large and strongly humped, not exceptionally broad; abdomen almost round, very slightly dorsoventrally compressed; head of medium size, hypognathous, with fairly large eyes placed dorsolaterally; abdomen tapering posteriorly, gills conspicuous, carried laterally away from the body, situated on segments 1-7, 1st 2 pairs relatively small, gills strongly lamellate with entire margins, anteroventral margin thickened and with spines towards the outer margin except for the 1st, gills with a large tuft of fibrils, posteriorly at base; 3 equal tail-filaments, the cerci plumed only on the inner side; tarsal claws simple, swollen at base, only slightly curved at apex; all legs rounded and without tufts or brushes of long setae; mouthparts abnormal, mandible with very reduced molar process, maxillary and labial palps multisegmented, maxilla with a number of apical, extremely long, curved spines.

This genus comes close to *Ameletopsis* Phillips from New Zealand but in the adult it differs in lacking a distinct triad on the deeply forked *MP* of the hindwing and in the distinctly 4-segmented claspers of the male. The nymph differs in having long setae only on the inner margins of the cerci and in minor details of segmentation of the maxillary and labial palps. The genus is known to occur from near Mackay in Queensland to the Kosciusko region of New South Wales.

Harker (1954) compares this genus with *Coloburiscoides* to which it bears a superficial resemblance.

KEY TO THE SPECIES OF THE GENUS MIRAWARA

Imagos

1. Wings pale brown with a purplish tinge; darker yellow-brown over costal and subcostal spaces; yellowish at base .... *megaloprepia*, sp. nov.
   Wings pale purple; yellow brown over costal and subcostal spaces; slightly yellowish at base .... *purpurea*, sp. nov.
   Wing hyaline; dark yellow brown, with almost black spots, over the costal and subcostal spaces; slightly yellowish at base .... *aapta* Harker

MIRAWARA MEGALOPREPIA, sp. nov.

Plate 1; Plate 2, Figs. 1-3

Female Imago

Head moderate, as wide as prothorax, reddish brown with some black markings; eye large, dark; ocelli pale, set in black; antenna very short, reddish; thorax reddish brown, mesoprescutum and postscutellar margins darker; mesopostscutellum projecting over the metanotum; legs reddish brown, dorsal surface of tarsi somewhat darker; tarsal segments decreasing regularly in length except in that the apical is longer than the preceding; 1st tarsal segment fused with the tibia; tarsus, including this fused segment, considerably longer than the tibia; tarsal claws small, markedly dissimilar, the sharp claw with a pronounced bulge on the inner side and strongly incurved apex; 2nd claw stout, dark, and with an obliquely truncate, apical margin.

Wings brilliant, the membrane completely coloured a rich pale brown with purplish hues except for the costal area which is a deep yellowish brown with 4 or 5 darker zones. The colouring is a little lighter towards the base and somewhat yellowish. Forewing with tornus beyond two-fifths of the wing-length from base; MP_2 arising close to the base and curving so as to run closer to CuA than to $1MP$; faint bullae about half-way along R_{4+5} and MP_1; hindwing triangular, apex rounded, caudal margin with a slight reentrant angle; humeral angle not strongly produced, rounded; costal crossveins numerous; Rs and MA forking before the middle of the wing; MP forking close to its base, without a distinctly developed triad.

Abdomen with segments rather short and broad, yellowish brown, the lateral and caudal margins with a wide dark border; medianly with a longitudinal brownish stripe and lateral to that an irregular darker longitudinal stripe, narrowing and straightening to the caudal segments; segment 9 with its posterolateral angles carrying a sharp, backwardly projecting spine extending almost as far as the caudal margin of segment 10; segment 10 much narrower than 9, small, a caudal lobe almost as long as the base of the segment and half its width extending over the very reduced appendix dorsalis; under surface of abdomen much paler, each segment with a pair of oblique, slightly curved dark lines and a pair of dark spots caudal to the lines; 2 tail-filaments, the appendix dorsalis very reduced, the cerci very long, about twice as long as the body, the basal portion dark, the apex white, slightly darkened at the joints; subanal plate excavated semicircularly on its distal margin, strongly bifid, with pointed lobes.

Length of body 17 mm; length of forewing 20 mm; length of cerci 36 mm.

Male Imago

Not known.

Subimago

The coloration of the two sexes differs markedly. Further, the male is only about two-thirds the size of the female.

Male Subimago

The body colour of the adult male, which is similar to that of the adult female, shows through the thin subimaginal skin.

Wings opaque, greyish, with numerous small, more or less rectangular, darker areas bordered by the main veins and the crossveins. This darkening is more pronounced towards the caudal margin of the hindwing and the apical margin of the forewing, where it forms more or less distinct transverse bands. There is also a complete band at the middle of the wing and other incomplete ones along the costal area. Costal space darker than the rest of the wing particularly so at the base of the wing.

Fore legs of the male only a little over half the length of the forewing; 2 tail-filaments, the cerci, which are much shorter than the body; eyes large, meeting in the midline.

Female Subimago

Considerably larger than the male. The adult coloration of the body shows below the thin subimaginal skin except over the abdomen where the subimago is uniformly dark grey.

Wings opaque, with a grey pattern similar to that of the male overlying the pale brown colouring of the imago and so obscured to some extent. (In the male the imago would have clear wings except for a slight darkening along the costal border.)

Fore legs relatively much shorter than in the male; the 2 tail-filaments relatively longer but not as long as the body.

Nymph

Shrimp-like, head slightly dorsoventrally flattened, thorax humped, abdomen rounded; legs rounded and without tufts of setae, gills on segments 1-7, held laterally away from the body, consisting of a greatly expanded lamella and a posterior, basal tuft of fibrils; eyes large, placed dorsally on the flattened head, labrum large, protruding; antenna longer than the head.

Mouth parts abnormal; mandible with extremely well-developed canines and very reduced molar process; molar process a slight obtusely pointed projection at the inner basal margin; canines in 2 groups, an apical very strong, gently curved, 3-pronged projection, the median prong somewhat longer than the subequal upper and lower prong; a second group, directed mesally, consisting of an anterior, stronger, almost straight, sharply pointed projection bearing a smaller prong on its ventral face; below these canines a much shorter, blunter projection bearing an apical tooth and a series of very much smaller teeth and setae on its posterior margin, decreasing in size away from the apex; maxilla very large, cardo and stipes quite distinct, a small, more heavily sclerotized area on the mesal border of the stipes, and demarcated from it, may represent a lacinia; galea as stout and long as the stipes, terminating in 5 very long, fine, gently curved and tapered, sharply pointed, articulated spines; these spines form two series, 4 form an outer vertical series, the most ventral being a little longer and more finely tapered than the others which are subequal and have the apex slightly hooked, the 5th is placed mesad to the outer series and is considerably shorter and finer; on the inner apical margin a small tuft of very short hairs; maxillary palp about as long as the galea and 14-segmented, the 2nd segment being considerably stouter and longer than the others which taper to a very fine apex; the labium with abnormally long and multisegmented palps, palps 15-segmented, the 1st segment very long and stout, the remaining segments forming a thin whip-like flagellum, not quite twice as long as the basal segment; mentum produced to acute points at the anterolateral corners, ligula with convex lateral margins, glossa and paraglossa quite distinct, longer than the ligula, the paraglossa constricted about its middle and appearing 2-segmented; paraglossa with a few setae on the outer margin of the apical half; hypopharynx with heavily sclerotized anterior margin, truncate, with rounded lateral margins, bearing dense fine setae over the sclerotized portion; superlinguae emarginate mesally before the rounded apex.

Colour varying from yellowish brown to dark brown, with darker markings, tips of caudal setae whitish, gills grey with fibrils black; face mostly dark and wing-sheath dark in fully grown nymphs.

Types.—Holotype ♀ imago and type ♀ subimago, Lamington National Park, Qld. (Jan. 1943, E. F. Riek); type ♂ subimago, same locality (Jan.

1944, E. F. Riek). Type nymph taken under rocks at the same locality (Jan. 1943, E. F. Riek). Types and a series of ♀ imago paratypes and numerous nymphs in the Division of Entomology Museum, C.S.I.R.O., Canberra. 1 ♀ paratype in George F. Edmunds Collection, Salt Lake City, Utah.

Type locality.—Upper Coomera River, Lamington National Park, Qld.

Distribution.—QUEENSLAND: Streams of the Lamington National Park; Netherdale, 35 miles W. of Mackay (A. N. Burns), 2000 ft. Possibly also Conondale (25.iv.1945, E. F. Riek) where nymphs only were collected.

The female subimago was reared from fully grown nymphs which require running or well-aerated water for their survival. The male subimago was taken clinging to the under surface of an overhanging log on an overcast day.

The species occurs in any of the fast-flowing streams in the area above about the 2000 ft level. The adult females fly in the middle of the day, only over the quiet, sheltered pools, and are rarely seen over the broken water. The shrimp-like nymphs are found both in the more slowly moving waters of the deep pools where they often rest on the upper surface of submerged rocks and in the swiftly flowing broken water where they cling to the under surface of boulders, preferably along the margins.

MIRAWARA PURPUREA, sp. nov.

Female Imago

Differs from *megaloprepia* only in coloration; head and thorax dark brownish rather than reddish brown; the abdomen reddish brown, the dark banding at the caudal and lateral margins of each segment narrow; segments with a pattern similar to that of *megaloprepia*; ventral surface of abdomen much lighter in colour than the dorsal.

Wings pale purple, costal area dark yellowish brown, slightly yellowish at bases of wings; cerci long but not twice as long as body, apex white.

Length of body 16.5 mm; length of forewing 18 mm; length of cerci 31 mm.

Male Imago

Not known.

Subimago

Not known.

Nymph

Not known definitely as two species of adult have been collected from the type locality of this species.

Type.—Holotype ♀ imago in the Division of Entomology Museum, C.S.I.R.O., Canberra.

Type locality.—Upper Cotter River, A.C.T. (8.ii.1947, E. F. Riek).

Distribution.—AUSTRALIAN CAPITAL TERRITORY: Cotter River. NEW SOUTH WALES: Styx River (1.iv.1950, E. F. Riek); Wee Jasper, Goodradigby River (7.xii.1950, E. F. Riek).

This species is very similar in general coloration and habits to *megaloprepia* but the pigmentation is less intense and of a slightly different colour.

MIRAWARA AAPTA Harker

Plate 1, Figs. 7 and 8; Plate 2, Figs. 4-6

Mirawara aapta Harker, 1954, Trans. R. Ent. Soc. Lond. 105: 261.

Female Imago

Wings hyaline except for the yellow-brown costal and subcostal spaces and for a slight yellowing at the bases; body colouring much as in *megaloprepia* but the head and thorax more brown with blackish markings; cerci black at base, becoming lighter in middle (and there only darkened at apex of segments) and white over almost the apical half.

Male Imago

Similar colouring to female but dorsal thorax mostly or all black; fore leg mostly dark except for coxa and base of femur, other legs yellowish brown; claspers darkened on external face except for basal half of 1st segment.

Cerci relatively longer than in female; clasper 4-segmented, 1st very long, 2nd to 4th very short, decreasing regularly in size; penis with a pair of simple lobes, apex pointed and incurved, upper surface near apex with a slight thickening.

Female Subimago

Wings opaque, brownish, with numerous small, more or less rectangular, darker areas bordered by the main veins and the crossveins. This darkening is more pronounced at the tornus and forms faintly darker transverse bands in the apical half of the forewing; also darker at caudal margin of hindwing. Costal space darker than the rest of the wing due to the underlying pigment of the imaginal wing. Tail-filaments about as long as the body, the apical half mostly pale.

Types.—Holotype ♂ imago, allotype ♀ imago, type subimago in the British Museum (ex Tillyard Collection).

Type locality.—Upper Murrumbidgee River, Adaminaby, N.S.W. (11.xii.1936, R. J. Tillyard).

Distribution.—NEW SOUTH WALES: Bolairo, upper Murrumbidgee River (11.iii.1951, E. F. Riek); Styx River (1.iv.1950, E. F. Riek); Mt. Garrick, Snowy River (Feb. 1909). AUSTRALIAN CAPITAL TERRITORY: Upper Cotter River (7.iii.1948, 28.ii.1948, E. F. Riek).

This species is distinguished readily by the hyaline wings of both sexes. At the Styx River and the upper Cotter River it is associated with *purpurea*. The males collected at Bolairo were taken swarming around a limited number of females settled on shrubs and long grass bordering deep open pools on the stream. Although flying at midday and slightly later, the males were caught fairly readily by hand. The nymphs form a significant part of the food of the introduced trout.

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Figs. 1-5.—*Mirawara megaloprepia*, sp. nov., mature nymph.

Fig. 1.—Flattened head split at dorsal suture; also displaced mandible and maxilla. × *c.* 5.

Fig. 2.—Mandible and maxilla enlarged. × *c.* 9.

Fig. 3.—Labium. × *c.* 9.

Fig. 4.—Tail-filaments. × *c.* 5.

Fig. 5.—Abdominal gill. × *c.* 9.

Fig. 6.—*Mirawara megaloprepia*, hind leg of adult female showing tarsal segmentation. × *c.* 5.

Figs. 7-8.—*Mirawara aapta* Harker, caudal portion of abdomen. × *c.* 9. (Fig. 7.) Apical portion. × *c.* 18. (Fig. 8.)

Fig. 9.—*Mirawara megaloprepia*, hindwing of adult female. × *c.* 5.

PLATE 2

Figs. 1-3.—*Mirawara megaloprepia*, sp. nov.

Fig. 1.—Holotype female, natural size.

Fig. 2.—Type female subimago, natural size.

Fig. 3.—Type male subimago, natural size.

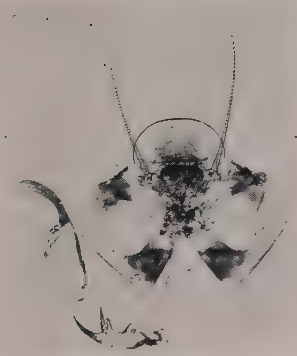
Figs. 4-6.—*Mirawara aapta* Harker.

Fig. 4.—Male, natural size.

Fig. 5.—Female, natural size.

Fig. 6.—Female subimago, natural size.

AUSTRALIAN MAYFLIES (EPHEMEROPTERA). I



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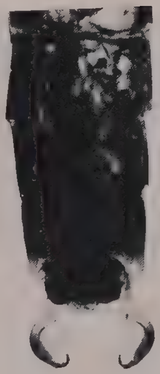

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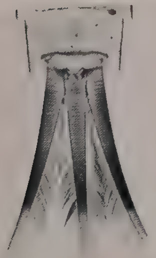

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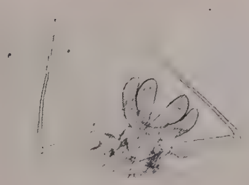

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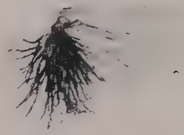

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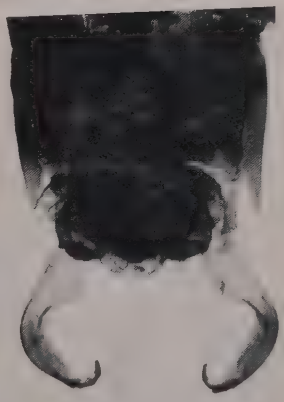

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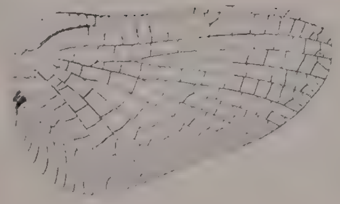

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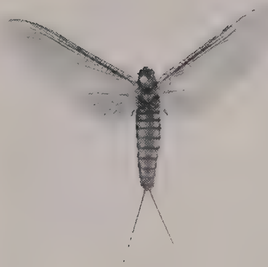
AUSTRALIAN MAYFLIES (EPHEMEROPTERA). I



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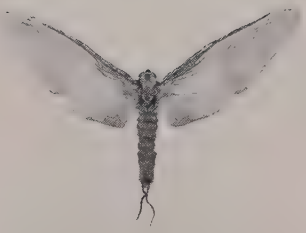

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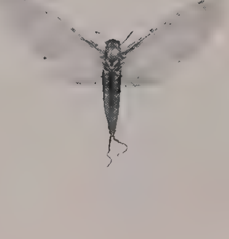

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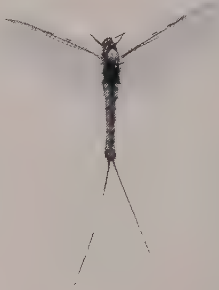

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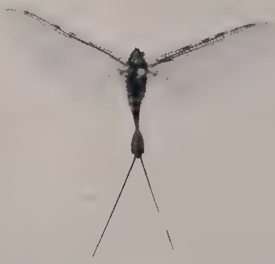

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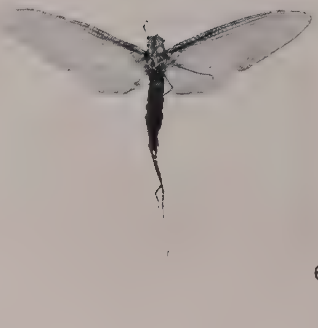

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THE AUSTRALIAN XIPHYDRIIDAE (HYMENOPTERA: SYMPHYTA)

By E. F. Riek*

(*Manuscript received November* 24, 1954)

Summary

The paper deals with the systematics of the Australian representatives of this small family of sawflies. *Austrocyrta australiensis*, gen. et sp. nov., of the subfamily Derecyrtinae, known previously only from South America, is described.

Introduction

This small family has a world-wide distribution with about 85 known species. It is very poorly represented in Australian collections. Only 10 specimens of the Australian species are known. Three species, now placed in *Rhysacephala* Benson, have been described from unique specimens. A new genus is erected for a new species allied to the South American *Steirocephala* Benson. This is the only record of the subfamily Derecyrtinae outside South America.

Family **XIPHYDRIIDAE**

Large insects, usually over 14 mm long. Antennae setaceous and 13- to 25-segmented, with a long curved scape at least as long as the 1st funicle segment. Neck long; cervical sclerites, viewed from the side, appear longer than broad. Mesonotum with a transverse furrow. Forewing corrugated apically and without an appendiculate cell; 2 interradial cross-veins present in most, and base of *Rs* not angled sharply near its base, so that its basal portion is not in a line with base of *M*. Tibiae without pre-apical spines; fore tibia with only one apical spur. Last abdominal segment without an apical horn-like projection.

All known larvae are wood-borers of deciduous trees and have only vestigial thoracic legs.

Benson (1954) has recently revised the classification of the family. The two subfamilies can be separated by the following key.

Key to the Subfamilies of the Family Xiphydriidae

Pronotal collar deeply excavated in front (so that the total excavation is several times deeper than the remaining medial length which itself is less than the length of a tegula); scutellum without any dorsal area defined by a carina and no prominent tubercle near its apex, though the whole may be coarsely sculptured .... Xiphydriinae

Pronotal collar less excavated in front (so that its total excavation is at most scarcely longer than the medial length remaining, which itself is several times the length of a tegula); scutellum with a dorsal area margined by a carina and including a prominent tubercle near its apex .... Derecyrtinae

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Genus AUSTROCYRTA, gen. nov.

Genotype *Austrocyrta australiensis*, sp. nov.

Allied to *Steirocephala* Benson but differing mainly in the shape of the pronotal collar which is shaped more as in *Derecyrta* but is produced caudally into a round eminence on either side of the meson, and in the hind tarsus which bears short rounded pulvilli. Apical (4th) segment of labial palp longer than the first segment, clavate. Antenna 25-segmented. Scape long, pedicel short but longer than wide, 3rd antennal segment (1st funicle) about as long as scape and only about as long as 4th and 5th segments combined. Malar depression on gena without a raised carinate margin.

AUSTROCYRTA AUSTRALIENSIS, sp. nov.

Plate 1, Fig. 2

Female

Black species marked with yellow; pronotum widely (laterally), all scutellum, segment 2 of abdomen widely (laterally), and hind tibia at basal third or so, yellow; tibiae and tarsi, particularly of fore leg, lighter in colour, not black.

Antenna with 25 segments, pedicel almost half scape, 1st funicle as long as scape, with parallel sides and not constricted at apex, 2nd funicle about two-thirds 1st, succeeding segments decreasing regularly in length and breadth, so that antenna tapers to a point; face strongly rugulose except widely at occiput and there glabrous; lateral ocellus twice as far from eye as from median; prosternum with the dorsal projections almost meeting at the meson and these dorsal areas strongly longitudinally rugose; pronotum vertically truncate, dorsal surface very short, with a pair of rounded projections close to meson, posterior margin only very slightly excavated at meson, lateral areas large and extending back to the tegula, in frontal view with the anterior excavation occupying about half its length; scutellum with a convexly raised, transverse carina at apex, with faint median and lateral carinae; postscutellum irregularly produced at meson and with a strong, oblique carina extending from spiracle to posterolateral margin; tergum of 1st abdominal segment not sclerotized at meson, irregularly punctate, but laterally almost glabrous; succeeding segments irregularly sculptured; abdomen slightly contracted at base, rounded at apex, 9th segment large, 10th very small, ovipositor valves exserted about the length of the apical segment.

Male

Yellow markings of pronotum, scutellum, and segment 2 of abdomen similar to those of female; all legs with about the basal third of tibia and apex of femur narrowly, yellow; segment 9 of abdomen with a large yellow patch on each side of meson.

Antenna with 21 segments but basal structure similar to that of female.

Types.—Holotype ♀ in the Division of Entomology Museum, C.S.I.R.O., Canberra, A.C.T.; allotype ♂ in National Museum, Melbourne, Vic.

Type locality.—Holotype, Brisbane, Qld. (20.ix.1942, I. F. B. Common); allotype, Beaconsfield, Vic. (8.xii.1923, G. F. Hill).

The holotype has the yellow areas discoloured red owing to prolonged contact with cyanide. A second female from Ringwood, Vic. (23.xi.1934, K. Guichard) in the National Museum shows a minute yellow spot laterally on segment 1 of abdomen and all tibiae are completely pale at base though only narrowly on fore and middle tibiae.

Subfamily **XIPHYDRIINAE** Benson

Genus RHYSACEPHALA Benson

Rhysacephala Benson, 1954, Trans. R. Ent. Soc. Lond. 105: 158.

Genotype *Xiphydria obtusiventris* Rohwer, 1918, Ann. Mag. Nat. Hist. (9) 2: 433.

The genus is distinguished from all other Xiphydriinae except *Moaxiphia* Maa by its long 7-segmented maxillary palps (about twice as long as labial palps). It is distinguished from *Moaxiphia* by the parallel inner orbits, the broader interantennal area in relation to clypeal length, the longitudinally divided temples behind the eyes, and the enlarged hind claws of the female (from Benson).

Three species, all based on unique specimens, have been described from Australia. There is also a species from Aru Is.

RHYSACEPHALA LEAI (Forsius)

Xiphydria leai Forsius, 1927, Rec. S. Aust. Mus. 3: 286.
Rhysacephala leai Benson, 1954, Trans. R. Ent. Soc. Lond. 105: 159.

Male

Thorax, abdomen, and legs completely red; head black and yellow; antenna black; mandible yellow except for the black teeth; face with an irregular median black stripe, widest at the ocelli and at some distance below them, narrowing abruptly towards the antennal insertions; clypeus all yellow; at the vertex the dark area is joined by the two oblique areas extending from the dorsomesal borders of the eye; posterior margin of the eye widely yellow but posterior margin of head darkened; wings clear, venation black.

Scutum with a distinct median sulcus; axillae meeting widely at the meson; postscutellum strongly developed into a low rounded projection; propodeum at meson glabrous, the glabrous area triangular and tapering anteriorly; antenna with 21 segments, scape stout and curved, pedicel more than half scape, 1st funicle very long, longer than scape, 2nd funicle about half 1st, succeeding segments decreasing slightly.

Type.—Holotype ♂ in the South Australian Museum, Adelaide.

Type locality.—Cairns district, Qld. (A. M. Lea). Only the holotype male is known.

RHYSACEPHALA OBTUSIVENTRIS (Rohwer)

Xiphydria obtusiventris Rohwer, 1918, Ann. Mag. Nat. Hist. (9) 2: 433.
Xiphydria obtusiventris Morice, 1918, Trans. Ent. Soc. Lond. 1918: 253.
Rhysacephala obtusiventris Benson, 1954, Trans. R. Ent. Soc. Lond. 105: 159.

Female

Mainly black; head all black; thorax black above, reddish brown below; abdomen reddish brown; legs all yellowish, including all coxae; antenna yellowish, darkened at apex of flagellum; tegula yellowish; wing evenly, lightly infuscated, pterostigma red-brown; mandible yellow except for teeth.

Antenna with 20 segments and pedicel only about half the scape, otherwise as *leai.*

Type.—Holotype ♀ in the British Museum.

Type locality.—Kuranda, north Queensland.

There is a second female, Mt. Glorious, Queensland (18.ix.1927, H. Hacker), in the Queensland Museum, Brisbane, on which the above description is based. This species can be separated readily from *leai* on colour. In *leai* the thorax, abdomen, and legs are all red and the head is black and yellow, while in *obtusiventris* the head and thorax are black, the abdomen reddish brown, and the legs all yellowish.

RHYSACEPHALA WILSONI Benson

Plate 1, Fig. 1

Rhysacephala wilsoni Benson, 1954, Trans. R. Ent. Soc. Lond. 105: 159.

Female

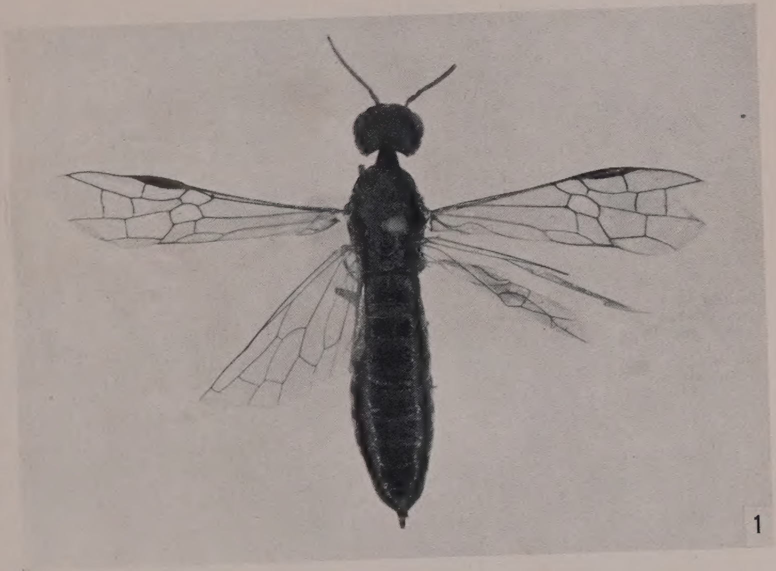
Black, marked with red and white; legs, except fore and middle coxae in part, all red; antenna all red, but scape and pedicel sometimes slightly darkened; mandible red, black at base and teeth; head all black; thorax all black except for narrow white posterolateral margin of pronotum and reddish black tegula; abdomen black with small white patches laterally on 3 to 8, largest on 8; wing very lightly infuscated.

Antennae damaged, up to 19 segments preserved, scape stout and curved, pedicel subquadrate, distinctly less than half scape, 1st funicle very long, longer than scape, 2nd a little more than half 1st, succeeding segments decreasing slightly; ovipositor valves only slightly exserted.

Type.—Holotype ♀ in the F. E. Wilson Collection.

Type locality.—Ringwood, Vic. (19.xi.1939, F. E. Wilson).

Specimens examined.—VICTORIA: Baxter (12.ii.1943, C. Oke), 3 ♀♀, National Museum, Melbourne (1 ♀ retained Division of Entomology Museum, C.S.I.R.O.); Millbrook, 1 ♀, National Museum, Melbourne.



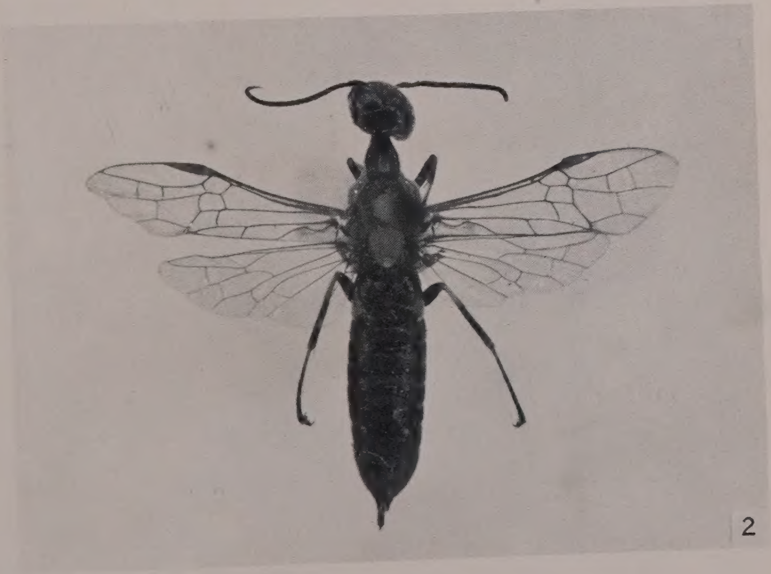


Fig. 1.—*Rhysacephala wilsoni* Benson. × *c*. 6.

Fig. 2.—*Austrocyrta australiensis*, gen. et sp. nov., holotype female. × *c*. 6.

The three females from Baxter were caught running rapidly on foliage. This species has red legs and antennae and white spots laterally on the abdomen and so is separated readily from the other two species.

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